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Food of American Plaice (*Hippoglossoides platessoides*) from the Grand Bank, Newfoundland

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Pitt, T. K. 1973. Food of American plaice (*Hippoglossoides platessoides*) from the Grand Bank, Newfoundland. J. Fish. Res. Board Can. 30: 1261–1273.

Invertebrates, principally benthic forms, occurred most frequently in plaice stomachs from the Grand Bank. Fish, almost entirely capelin and sand lance, however, contributed the greatest proportion of total weight: 85% on the southeast part of the bank (ICNAF Division 3N) and 55% in the northeast section (ICNAF Division 3L).

A seasonal feeding cycle was difficult to document because of the lack of winter samples, however, a greater proportion of empty stomachs occurred in February and March. The greater average weight of contents in spring samples (April–June) in Division 3L and in fall samples (October–November) for Division 3N was probably related to the availability of capelin and lance. The greater annual consumption of capelin and lance in Division 3N apparently accounted for the estimated higher caloric values of the average contents in this division than in Division 3L.

Pitt, T. K. 1973. Food of American plaice (*Hippoglossoides platessoides*) from the Grand Bank, Newfoundland. J. Fish. Res. Board Can. 30: 1261–1273.

Les organismes rencontrés le plus souvent dans les estomacs de la plie canadienne du Grand banc sont des invertébrés, en grande partie benthiques. Cependant, les poissons, presque exclusivement capelan et lançon d'Amérique, contribuent la plus grande proportion du poids total: 85% dans la partie sud-est (division 3N de l'ICNAF) et 55% dans le secteur nord-est (division 3L) du Grand banc.

A cause du manque d'échantillons en hiver, il est difficile de démontrer un cycle alimentaire saisonnier, mais on observe une plus grande proportion d'estomacs vides en février et mars. Un poids moyen plus élevé des contenus stomacaux dans les échantillons de printemps (avril–juin) dans la division 3L et dans les échantillons d'automne (octobre–novembre) dans la division 3N est probablement lié à la disponibilité du capelan et du lançon. Les valeurs calorifiques plus élevées des contenus stomacaux moyens la division 3N que dans la division 3L semblent attribuables à une plus grande consommation de capelan et de lançon dans ce secteur que dans la division 3L.

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As part of a detailed study of the biology of American plaice (*Hippoglossoides platessoides*) in the Northwest Atlantic, this paper presents information on the type and quantity of food taken by this species on the Grand Bank. The areas of the Grand Bank sampled included the north and northeast sections (International Commission for the Northwest Atlantic Division 3L) and the southeast section (ICNAF Division 3N) (Fig. 1); these areas being the location of the major fishery for plaice in the Northwest Atlantic. These two ICNAF Divisions represent a total possible habitat for plaice in excess of 40,000 square nautical miles. A comparison of food taken by plaice from the two divisions is presented.

The only detailed food study of *Hippoglossoides* was by Komarova (1939) for the Barents Sea. Except for Yanulov's (1962) brief reference to plaice food for ICNAF Division 3L and some information on plaice food and feeding in the Gulf of St. Lawrence by Huntsman (1918) and Powles (1965), no detailed study on food and feeding of this species in the Northwest Atlantic has been published.

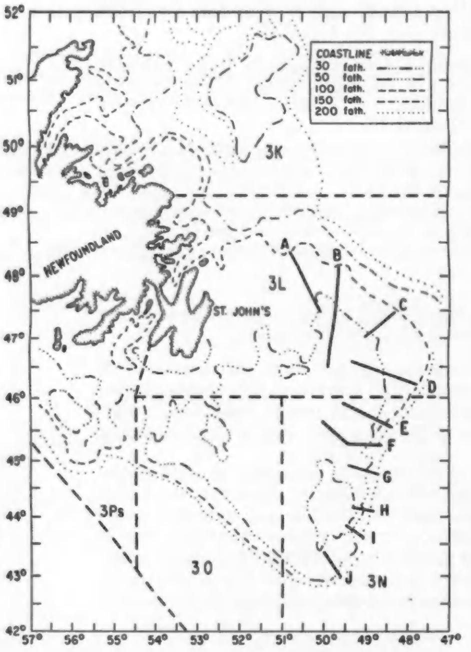

FIG. 1. Map of the area showing the ICNAF Division and the sampling transcepts mentioned in the text.

Materials and Methods

About 5000 stomachs were collected from 1964 to 1971 on cruises of the research ship *A. T. Cameron* which used a 41-5 otter trawl. For all years except 1971 sampling stations were on transcepts (Fig. 1) across the slope of the bank at 20-fath (37-m) depth intervals from 40 to 150–160 fath (73–290 m). Shallower than 40 fath, stations were normally placed between 10 and 15 miles apart. In 1971 the fishing stations were selected randomly from a number of strata into which the whole area was divided (Grosslein and Pinhorn 1971).

Stomachs were collected from a limited number of fish from each set in 5-cm length categories. In the analysis of data by length, samples were combined in 10-cm groups. Stomachs were removed from the fish almost immediately following capture, injected with a 5–10% solution of formalin and preserved in a similar solution for later examination. Length, sex, and maturity were recorded for the sampled fish. Stomach contents of each fish were separated into individual items and damp weights were determined to an accuracy of 0.01 g.

Some of the invertebrate organisms (particularly annelids and crustaceans) could be classified only to order or phylum, mainly because of digestive action, but this was no drawback since the primary objective was to classify the contents according to major groups with the classification to species being of lesser importance.

Because the sampling occurred at various localities at different seasons over a number of years, the general procedure was to combine the data for all years and thus present the overall or average feeding conditions for the areas under consideration. However, a comparison of the food taken in different years for the same locality and month was made. In 1967 approximately 50 sets were made in Division 3L in June on the four lines or transcepts in this division (A–D, Fig. 1) and included day and night catches. These stomachs were compared to data collected in the same period in 1971 from randomly selected fishing stations. For Division 3N the only good comparison was for October 1964 and 1968 when a relatively small area of the southeast slope, including transcepts E, F, and some of the area between (Fig. 1), was fished rather intensively.

To present and compare the diet of plaice in the two ICNAF Divisions and for seasonal differences the percentages of fish containing the various items (occurrence) were calculated using the total number examined including empty stomachs. To compare the relative importance of the various food items, the percentage that each represented of the total contents was also calculated. Additionally, particularly for seasonal comparisons, the mean weight of the total food for each length group was calculated.

Since weight of contents was used to compare all fish sampled for each season, the inclusion of empty stomachs (zero contents) was considered necessary to give values for the size-groups that were representative of the stock as a whole including both the feeding and nonfeeding fish. The inclusion of zero contents, however, presented some difficulty; hence, a transformation of the weight of contents to a logarithmic scale, as suggested by Barnes (1952) for certain biological data, appeared appropriate. The transformation actually used was 100 (Log weight + 1).

The combination for seasonal differences for the principal food components were as follows: Period I — fish collected in March only in Division 3L and February only for 3N; Period II — April–June samples; Period III — July–September samples; and Period IV — October and November samples. These were the only months for which data were available.

A comparison of a small number of fresh and formalin-preserved sand dollars, starfish, and clams gave changes in weight varying from 97 to 103% of the fresh condition after preservation in seawater formalin for 1–2 months. Capelin preserved in 10% formalin were 97–99% of their original weight after 30 days. The weight of the formalin-preserved material was therefore treated as fresh or live weights for estimating rough caloric values of the food.

The caloric values for live weights of the different phyla from Brawn et al. (1968) were applied to the weights of the various major food items recovered from the stomachs. Although some of the species present in Grand Bank plaice were not recorded in the latter paper it was assumed that average phyla values would be appropriate for this presentation. Brawn et al. (1968) calculated a value of 1927 cal/g wet weight for herring with 6.6% fat and 1085 cal/g for a cunner. Partly spent capelin contain 3–4% fat (Andrews 1954) and lance probably less than this so that a rough value of 1.75 kcal/g was used.

Results

DIET COMPOSITION

Invertebrates, principally benthic forms occurred most frequently in plaice stomachs with fish being next in frequency of occurrence, however, as a percentage of the total food weight, fish far surpassed all the other groups (Fig. 2).

Echinoderms were the principal invertebrate group and were represented almost entirely by the brittle stars, (*Ophiura sarsi* and *O. robusta*), the sand dollars, (*Echinorachinus parma*), and sea urchins, (*Strongylocentrotus droehbachiensis*). Representatives of most of the main orders of Crustacea occurred, however, the most frequently occurring orders were Amphipoda, Euphausiacea, Cumacea, and Decapoda. Many of the crustaceans were not

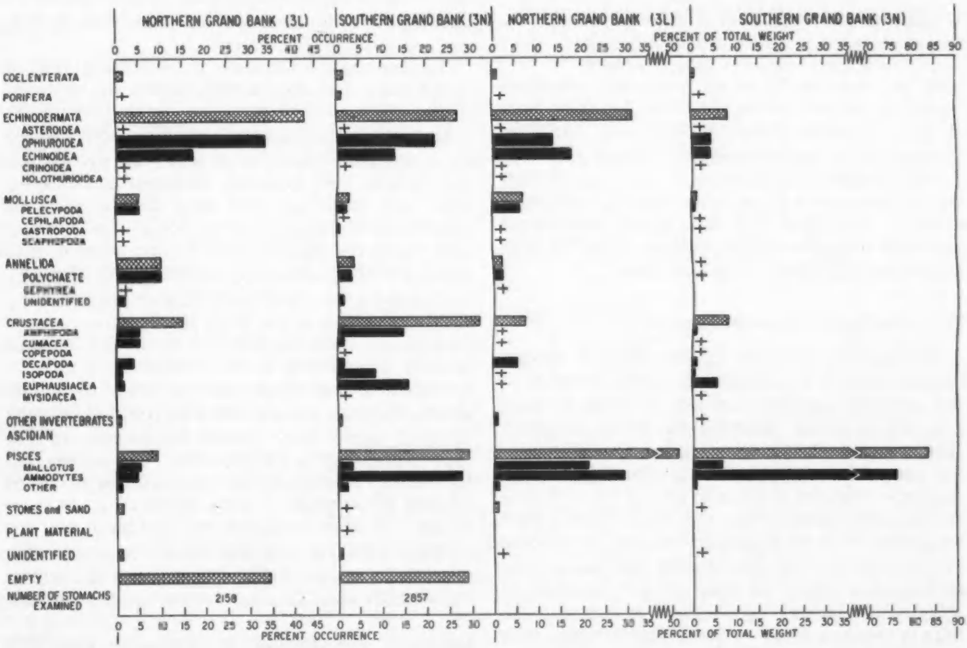

FIG. 2. Diet comparisons of plaice for ICNAF Divisions 3L and 3N. Percent occurrence calculated from the total number of fish examined for each division and percent of total weight calculated from the total weight of the food for each division. (Phyla or other totals cross-hatched, + = < 1.0%.)

identified. However, in the amphipods *Stegocephalus* sp., *Haploops* sp., and *Caprella* sp. were tentatively identified. The euphausids *Thysanoessa* sp. and *Meganyctiphanes norvegica*, the cumacean *Diatylis* sp., and decapods *Hyas araneus*, *Hyas coarctatus*, *Pandalus borealis*, and *Pandalus montagui* were noted. Isopods, copepods, and mysids occurred in relatively few stomachs. Almost all of the annelids were from the order Polychaeta with both free-living and burrowing or tube-building forms being represented in approximately equal quantities. A few gephyreans were also recorded in the northern area. Most of the molluscs were bivalves (Pelecypoda). *Nucula tensis*, *Siliqua* sp., *Nuculana tenuisulcata*, and *Serripes groenlandicus* were identified. Coelenterates consisted mostly of sea anemones and a few hydroids.

Fish consisted almost entirely of northern sand lance (*Ammodytes dubius*) and capelin (*Mallotus villosus*). Other species of fish were found, but only the mailed sculpin *Triglops murrayi* occurred to any substantial degree.

Diet Variations in Different Years From the Same Areas

Table 1a shows that for Northern Grand Bank, the most obvious differences between the 2 years were the greater selection of echinoderms in 1967 and the significantly larger proportion of empty stomachs encountered in 1971. For the other items of diet, except for specific differences at particular size-groups no major trends were present.

For Southeast Grand Bank, (Table 1b) the only major difference was the more frequent occurrence of fish in the diet in 1964. Significantly more empty stomachs were also encountered in 1968. For other food items, differences were not great.

Food Variation Between Areas

Disregarding fish size for the moment, echinoderms occurred in significantly more stomachs in the northern samples (Division 3L) than in those from the southeast (Division 3N) ($P = < 0.001$). (Fig. 2 and Table 2). Echinoderms also accounted for a significantly higher proportion of the total weight in Division 3L than in 3N, ($P = < 0.001$). Brittle stars (Ophiuroidea) (33.3%) occurred most frequently of all the organisms recorded in Division 3L followed by the sand dollars and sea urchins (Echinoidea). Both of these groups occurred in significantly greater proportions in Division 3L than in Division 3N ($P < 0.01$). Significantly more fish in Division 3L also contained molluscs and annelids ($P = 0.03$) and accounted for significantly higher proportions of the total food taken.

Fish and Crustacea, the two other major food groups, were represented in significantly higher proportion in the southeast areas (Division 3N) ($P < 0.001$) (Fig. 2 and Table 2). Within the crustaceans only cumaceans and decapods were represented in a substantially greater number of fish in the nothern area (Division 3L) than in Division 3N ($P = 0.01$), however, the quantities taken were relatively small in both areas. Fish occurred in 29.6% of the Division 3N stomachs and accounted for 83% of the total weight of food. Both of these percentages were significantly different from Division 3L ($P < 0.001$) where fish occurred in only 9.1% of the stomachs and accounted for 51.9% of the total weight. Significantly more plaice select capelin (*Mallotus*) in Division 3L (5%) than in 3N (3%) ($P = 0.01$) and account for 20% of the food as compared to about 6% in the southeast area ($P = < 0.001$). Sand lance (*Ammodytes*), however, were much more important in Division 3N, occurring in 27.8% of the stomachs and accounting for over 80% of the total food weight against an occurrence of 4.2% and about 30% of the total weight in Division 3L ($P < 0.001$ in both cases). There were significantly more empty stomachs in Division 3L ($P = 0.002$), however, these will be dealt with in presenting seasonal differences.

Taking size of fish into consideration (Fig. 3 and Table 2) the same general pattern was observed as for all sizes combined (Fig. 2). In Division 3L echinoderms, molluscs, and annelids were selected by significantly more fish in nearly all size-groups. In Division 3N, however, although echinoderms were still important, fish and crustaceans were selected more frequently by all size-groups in which they occurred. No fish, molluscs, or annelids were selected by the 10-cm group in Division 3N (Table 2).

Except for the significantly higher percentage by weight of capelin in the 20–29 and 30–39-cm groups in Division 3L the distribution by weight followed roughly the pattern as the occurrence (Table 2). Generally greater percentages by weight of echinoderms, molluscs, and annelids were found in Division 3L and significantly greater percentages of fish and crustaceans in Division 3N. The distribution by weight of echinoderms and molluscs remained roughly the same at all sizes. However, an increase in the consumption of fish with predator size was coupled with the opposite trend for crustaceans (Fig. 3). Except for the 10–19-cm group in Division 3L, annelids were taken in relatively small quantities.

Seasonal Differences in Stomach Contents

In Division 3L there was no consistent pattern of seasonal differences in the percent occurrence or in the mean weight of the total of the contents (Fig. 4 and Table 3). March data came from so few stomachs as to be relatively meaningless with regard to the occurrence of the different items. There was a significantly higher percentage occurrence of echinoderms at 50–59 cm and lower occurrence of Pisces at 40–49 cm between the April–June and July–September data ($P = 0.04$ and 0.05, respectively). There was a significant increase in the occurrence of empty stomachs during October and November in the 30–39 to 50–59-cm group. Generally speaking the smallest quantities occurred in October–November and disregarding the March data (with large errors) the greatest quantities usually occurred in the spring (April–June).

In Division 3N the most obvious seasonal difference was the significant increase in the occurrence of Crustacea and fish during July–November (Fig. 5 and Table 3). Echinoderms were selected primarily during the April–June period. As in Division 3L a substantial proportion of the stomachs collected during February were empty although the numbers

TABLE 1. Percent occurrence and percent of total weight of major food components of plaice from ICNAF Division 3L for stomachs collected June 1967 and 1971, and for Division 3N for October 1964 and 1968. An asterisk indicates significantly higher percent at the 5% level.

	10–19 cm		20–29 cm		30–39 cm		40–49 cm		50–59 cm		60–69 cm	
Food type	% occurrence	% total wt	% occurrence	% total wt	% occurrence	% total wt	% occurrence	% total wt	% occurrence	% total wt	% occurrence	% total wt
						ICNAF Division 3L 1967 and 1971[a]						
Echinodermata	8.3	6.2	34.0	45.2*	64.5*	55.8*	65.5*	23.6	65.2*	33.3	69.2*	72.3*
	33.3*	36.8	29.2	27.1	36.5	45.3	40.6	28.2*	39.3	35.3	27.3	33.1
Mollusca	–	–	4.2	4.8	9.0*	6.6*	5.6	1.7	8.7	2.5	15.4	5.5
	3.3	13.1	2.2	0.8	2.3	1.5	8.1	28.1*	7.1	6.8*	18.1	45.8*
Annelida	8.3	18.8	10.6	5.3	10.7	2.9	9.9	0.7	7.2	0.2	7.7	0.2
	13.3	18.5	10.1	13.1	8.7	6.8*	8.1	1.7	6.0	2.4*	9.1	1.0
Crustacea	41.7	75.0	40.4*	40.4*	24.3*	5.1	14.8	0.2	11.6	0.1	7.6	0.5
	20.0	31.6	13.5	17.0	11.9	9.3	13.0	16.3*	7.2	36.0*	9.1	13.8*
Pisces	–	–	1.1	4.0	4.0	29.0	21.1*	73.7*	14.5	62.9*	7.7	21.5*
	–	–	2.2	41.2*	4.8	32.2	6.5	21.6	8.3	19.1	9.1	6.2
Empty	41.7	–	29.8	–	18.1	–	17.6	–	20.3	–	15.4	–
	30.0	–	53.9*	–	47.6*	–	37.4*	–	40.4*	–	43.5*	–
Totals (No. of stomachs and wt of contents g)	12	1.6	94	37.6	177	253.4	142	1266.8	69	1037.1	13	116.2
	30	3.8	89	38.8	126	151.1	123	554.9	84	668.7	11	198.8
						ICNAF Division 3N 1964 and 1968[b]						
Echinodermata	–	–	21.0	3.5	19.0	1.3	13.0*	0.4	16.6*	1.6	21.1	1.4
	–	–	9.7	1.5	10.7	1.2	1.8	3.9*	6.7	1.7	–	–
Mollusca	–	–	–	–	–	–	–	–	0.6	0.06	–	–
	–	–	–	–	1.8	+	–	–	2.0	0.20	–	–
Annelida	–	–	–	–	–	–	1.3	0.05	–	–	–	–
	–	–	–	–	7.1*	0.7	3.6	0.15	–	–	–	–
Crustacea	–	–	75.6	84.6	65.3	24.4	45.8*	3.5	25.5*	1.0*	42.1**	1.2**
	–	–	64.5	98.5*	60.7	55.5*	32.7	8.5*	6.7	0.3	–	–
Pisces	–	–	7.6	11.9*	51.6*	74.3*	79.1*	55.1	86.6*	55.7	89.5*	97.4
	–	–	–	–	17.9	41.9	56.3	91.3*	51.1	97.8*	44.4	100*
Empty	–	–	19.3	–	12.8	–	10.8	–	10.1	–	–	–
	–	–	29.0	–	23.2*	–	18.2	–	44.4*	–	55.6*	–
Totals (No. of stomachs and wt of contents g)	–	–	119	272.2	242	2208.1	306	12614.1	157	7940.5	19	1549.8
	–	–	31	48.0	56	247.8	55	901.7	45	891.4	9	338.4

[a] Upper and lower figures represent 1967 and 1971 data, respectively.

[b] Upper and lower figures represent 1964 and 1968 data, respectively.

collected were relatively small. Significantly smaller average amounts of food were taken in February at all size-categories than at any other period; on the other hand significantly greater average weights were reached for the fall (October–November) data. No significant difference was observed between the April–June and July–September averages (Table 3).

CALORIC VALUE OF STOMACH CONTENTS

Log–log regression of mean caloric value per 100 fish vs. fish size (midpoint of the 10-cm length group) were made and covariance tests performed for seasonal data and for the total of each ICNAF Division (Fig. 6). The rate of increase with length in the caloric value of stomach contents per 100 fish examined indicated a similarity between data collected for the two ICNAF Divisions during the April–June period only (F = 0.81 and 0.01 for slope and adjusted means, respectively, for F_{05} = 5.12). For the other two periods and for the totals, an analysis of covariance indicated significant differences between the regression coefficients for the two Divisions (F = 6.38 for July–September,

TABLE 2. Detailed comparison of the (A) percent occurrence and (B) percent of total weight of food for each length-group for occurrence calculated from total no. examined.

	(A) Percent occurrence										
	10–19 cm		20–29 cm		30–39 cm		40–49 cm		50–59 cm		60–69
Food type	3L	3N	3L	3N	3L	3N	3L	3N	3L	3N	3L
Coelenterata	0.9	–	0.9	0.6	2.0	0.9	1.9	1.3	1.8	1.7	–
Porifera	–	–	0.2	0.6	–	0.9	0.2	0.7	0.3	0.2	–
Echinodermata	17.5	8.3	32.1*	26.0	47.6*	29.9	47.3*	25.9	47.6*	26.8	55.6*
Asteroidea	–	–	–	–	–	0.1	0.2	0.1	0.3	–	–
Ophiuroidea	17.5	12.5	28.7	21.5*	37.2*	21.2*	35.2*	19.2	32.6*	18.6	41.3*
Echinoidea	–	–	4.5	8.0*	15.7*	11.5	23.8*	10.7	25.4*	13.2	30.4
Crinoidea	–	–	–	–	–	0.1	–	0.3	0.3	–	–
Holothuroidea	–	–	–	–	0.2	–	–	–	–	–	–
Mollusca	–	–	2.2	1.4	4.7*	2.7	11.6*	2.6	9.5*	3.3	10.8
Pelecypoda	–	–	2.0	1.2	4.6*	2.6	5.6*	2.0	9.0*	2.5	10.9
Cephalopoda	–	–	–	–	–	–	–	0.1	–	–	–
Gastropoda	–	–	0.2	1.05	0.3	0.1	0.3	0.5	0.6	0.8	–
Scaphlopoda	–	–	–	–	–	–	–	–	0.3	–	–
Annelida	13.9*	–	10.8*	2.5	10.5*	3.7	9.6*	2.1	7.5*	2.7	4.3
Polychaeta	13.9*	–	10.8*	2.5	10.3*	3.7	9.4*	2.1	7.2*	2.7	4.3
Gephyrea	–	–	–	–	0.2	–	0.2	–	0.3	–	–
Unidentified	–	–	–	–	–	–	–	–	–	–	–
Crustacea	20.4	29.2	23.1	45.9*	16.2	40.5*	11.4	27.8*	7.8	15.3*	4.3
Amphipoda	9.3	25.0*	9.6	27.5*	6.4	20.5*	2.2	6.7*	0.6	4.4*	–
Cumacea	6.4	4.2	8.7*	3.5	6.6*	1.7	2.9*	0.3	1.5*	–	–
Copepoda	–	–	–	0.2	–	0.1	–	–	–	–	–
Decapoda	–	–	2.9	1.0	2.9*	0.7	5.6*	1.2	4.8*	0.8	2.1
Isopoda	–	–	0.7	6.4*	1.6	9.9*	1.3	8.2*	0.9	6.1*	2.2
Euphausiacea	5.6	–	3.4	19.0*	0.8	19.1*	0.3	16.2*	–	6.7*	–
Mysidacea	–	–	–	–	–	0.2	–	–	–	–	–
Other Inv.	1.9	–	1.1	–	0.8	0.7	0.5	0.2	0.9	0.4	–
Ascidian	–	–	–	–	<0.1	–	–	–	–	–	–
Pisces	–	–	3.4	3.5	7.6	22.7*	15.5	40.4*	11.7	49.4*	6.5
Mallotus	–	–	1.8	0.6	5.1	3.7	9.0*	2.9	4.2	4.0	–
Ammodytes	–	–	0.4	1.0	2.1	17.1*	7.7	37.9*	8.0	46.4*	6.5
Other	–	–	1.1	1.7	0.5	2.4*	0.2	0.9	–	0.2	–
Sand, stones, and plants	0.9	4.2	–	–	0.3	0.1	1.5	–	2.7*	0.4	0.1
Unidentified	0.1	–	0.1	0.1	–	–	–	–	–	–	–
Empty	46.3	66.7	38.3	33.9	34.1*	28.2	32.0	28.5	32.3	26.9	30.4
No. of stomachs	108	24	446	484	630	862	594	907	334	478	46
or wt of contents	–	–	–	–	–	–	–	–	–	–	–

15.39 for October and November, and 8.40 for the totals for $F_{05} = 5.12$) with the values being lower for Division 3L than for 3N.

Discussion

American plaice are normally caught at or near the bottom of the sea, but there is ample evidence that they also assume pelagic habits and move to shallower water layers at night (Beamish 1966; Woodhead 1966 and Pitt 1967a). The stomach contents of Grand Bank plaice, while they contained such benthic forms as echinoderms and pelecypods, also contained pelagic forms; euphausids, amphipods, and capelin. Sand lance (*Ammodytes*), a major food item, are known to make vertical diurnal movements although they usually inhabit the benthic region.

Groot (1969 and 1971) apparently considered *Hippoglossoides platessoides* to be a fish-feeder. This was based primarily on the structure of the alimentary canal, gill rakers, and the eye size. He considered this species to be one of the most active feeders of the Pleuronectidae, utilizing primarily visual stimulation for day feeding, but apparently

the various food types, ICNAF Divisions 3L and 3N. Asterisks indicate significantly greater amounts at the 5% level. Percent

(B) Percent of total weight at each size-group

cm	10–19 cm		20–29 cm		30–39 cm		40–49 cm		50–59 cm		60–69 cm	
3N	3L	3N	3L	3N	3L	3N	3L	3N	3L	3N	3L	3N
2.1	0.1	–	0.9	0.2	1.3*	0.5	0.6	0.4	0.7	0.6	–	6.5*
–	–	–	0.3	0.3	–	0.1	<0.1	<0.1	–	<0.1	–	–
32.0	23.2	18.2	28.1*	11.2	32.4*	8.7	23.1*	6.3	36.2*	7.2	52.5*	13.8
–	–	–	–	–	–	–	0.1	–	<0.1	–	–	–
16.4	23.8	–	23.6*	7.4	20.5*	4.4	10.7*	3.4	13.1*	3.5	20.2	5.2
31.6	–	–	4.8	3.8	12.1*	4.3	12.7*	2.9	23.2*	3.7	32.0	8.4
–	–	–	–	–	–	–	–	–	<0.1	–	–	–
–	–	–	–	–	<0.1	–	–	–	–	–	–	–
9.3	–	–	2.4*	0.5	2.7*	0.5	6.1*	0.6	5.6*	0.7	21.7*	3.0
8.2	3.7	–	2.3*	0.5	2.4*	0.5	5.4*	0.5	5.5*	0.6	21.7*	2.9
–	–	–	–	–	–	–	–	<0.1	–	–	–	–
1.0	–	–	<0.1	–	0.3*	<0.1	0.7*	<0.1	<0.1	0.1	–	<0.1
–	–	–	–	–	–	–	–	–	<0.1	–	–	–
2.1	26.4	–	11.3*	0.6	5.0*	0.4	1.6*	0.1	1.0*	0.1	0.3*	<0.1
2.1	26.4	–	11.3*	0.6	5.0*	0.4	1.5*	0.1	1.0*	<0.1	0.3*	<0.1
–	–	–	–	–	<0.1	–	0.1	–	<0.1	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–
14.4*	42.0	72.7	30.8	71.6*	4.5	24.0*	4.9	7.5*	8.9*	1.7	3.7	4.9
1.0	9.7	–	8.1	10.4	1.3	2.3*	0.1	0.4*	<0.1	0.1	–	0.2
–	14.1	–	5.7*	1.3	0.8	<0.1	<0.1	<0.1	<0.1	–	–	–
–	–	–	–	<0.1	–	<0.1	–	–	–	–	–	–
4.1	–	–	10.3*	2.1	2.1*	0.5	4.2*	1.0	8.9*	0.7	3.7	2.9
1. 0	–	–	0.2	1.2	–	–	<0.1	–	<0.1	–	0.6	–
8.2*	19.4	–	6.8	57.1*	0.1	20.3*	0.5	5.4*	–	0.7*	–	1.7*
–	–	–	–	–	–	0.2	–	–	–	–	–	–
–	2.2	–	0.9	–	<0.1	0.1	0.1	<0.1	0.2*	<0.1	–	–
–	–	–	–	–	<0.1	–	–	–	–	–	–	–
33.0*	–	–	24.8*	14.9	53.3	65.3*	61.6	84.8*	46.1	89.6*	21.8	77.2*
5.2	–	–	14.3*	2.2	38.4*	8.5	29.8*	4.6	11.4*	6.0	–	10.1*
28.9*	–	–	7.6	9.7	14.1	54.3*	32.4	79.5*	34.9	83.2*	21.6	67.1*
1.0	–	–	3.1	2.8	1.1	2.4	0.4	0.6	–	0.1	0.3	0.1
–	<0.1	–	0.1	0.1	<0.1	–	0.3	–	0.9	–	0.3	–
–	<0.1	–	<0.1	<0.1	–	–	–	–	–	–	–	–
26.8	–	–	–	–	–	–	–	–	–	–	–	–
97	–	–	–	–	–	–	–	–	–	–	–	–
–	13.4	1.1	193.8	486.5	1109.8	3516.9	3738.2	11352.3	3164.7	12705.2	744.2	3055.2

also using chemical stimulation especially at night. The evidence presented here clearly demonstrates the importance of fish to the diet of this species accounting for 50–83% of the total weight of the food (Fig. 2). Most reference to the food of adult American plaice by Huntsman (1819) and Powles (1965) for the Gulf of St. Lawrence and Bigelow and Schroeder (1953) for the Gulf of Maine listed echinoderms, crustaceans, and molluscs as the principal diet and Yanulov's (1962) brief reference to Division 3L plaice food and feeding gave echinoderms, polychaetes, and pelecypods as the major food items. In the Barents Sea, however, Komarova (1939) indicated that while benthic forms were very important as a food for this species, fish, primarily capelin, cod, and haddock were also of major importance.

Differences in the occurrence and relative amounts of the food items for the different years from the same ICNAF Divisions (Table 1) point to the

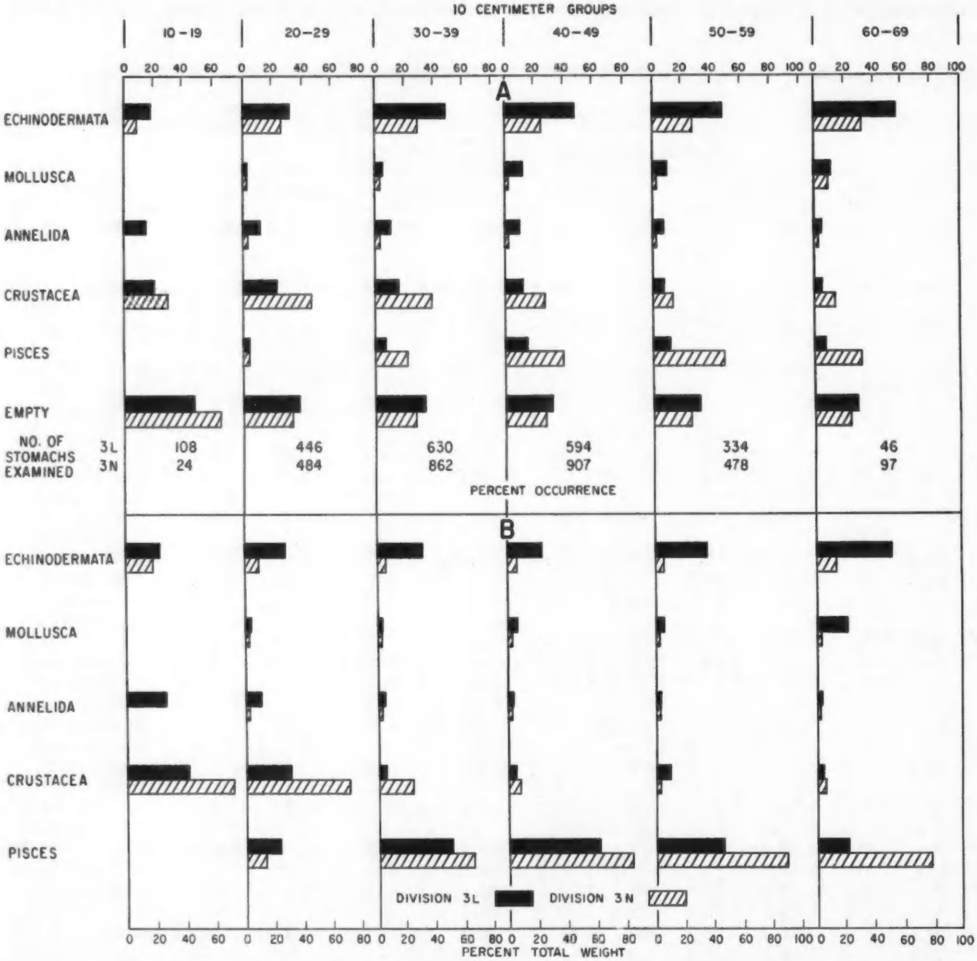

FIG. 3. Percent occurrence (A) and percent of the total food (B) at various size-groups for the major food components of plaice from ICNAF Divisions 3L (solid) and 3N (hatched). Occurrence = (No. of fish in which item appeared/Total no. examined at each size category) × 100. Percent of total weight = (Weight of particular item/Total weight of food for size category) × 100.

variability of the data within the areas. Annual hydrographic differences probably affect the availability of pelagic and semi-pelagic forms. Pitt (1969) showed that plaice on the Grand Bank were relatively sedentary with most returns from tagging experiments coming from localities less than 30 miles from the release site up to 6 years after release. Thus while for management purposes the Grand Bank plaice can be treated as two stocks (Divisions 3L and 3N), within these main stocks there appear to be many localized groups. The best indication of the total feeding regime of plaice on the Grand Bank probably comes from samples collected from a number of years for as much as possible of its total range.

The fact that capelin and lance occurred in a significantly greater proportion of the stomachs in Division 3N (29.6%) than to the north (Division 3L) (9.1%) was probably just a function of the size of the habitat and the relative availability of the prey species. On the southeastern portion of the bank (Division 3N) both the predator and prey beyond the 50-fath (91-m) contour, are concentrated on a relatively steep slope and are presented with rather narrow temperature zones, whereas to the north in Division 3L with a larger area (Fig. 1) and a very gradual slope the probability of an encounter between the predator and prey was much less. The same perhaps applied to pelagic or semi-pelagic crustaceans which occurred most

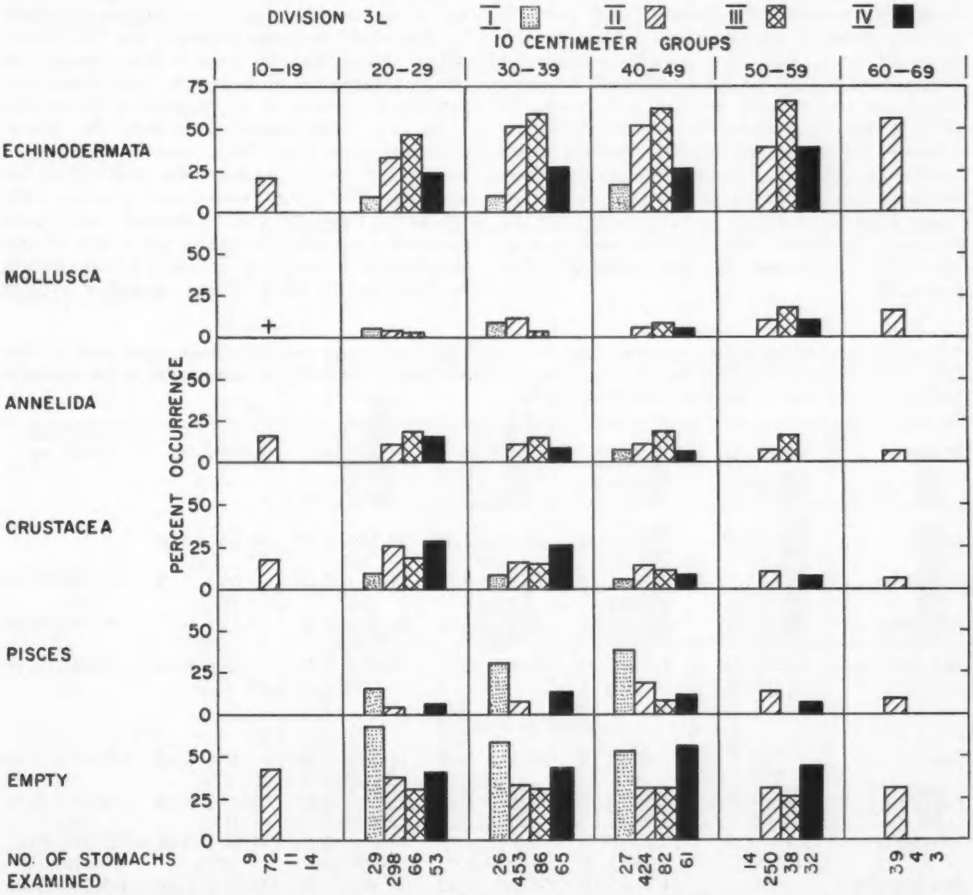

FIG. 4. Seasonal differences in food occurrence for ICNAF Division 3L. (I = March, II = April–June, III = July–September, IV = October and November.) Percentages were not calculated for less than 15 fish. (+)

frequently in the southern samples. The special importance of echinoderms in Division 3L was evident; they accounted for about 30% of the total weight of the food there as compared to less than 10% in Division 3N. Other evidence of the greater dependence on benthic forms in Division 3L was the more frequent occurrence, and a larger percentage of the total weight of pelecypods and polychaetes.

The primary difficulty in comparing seasonal differences in food intake was the possibility of annual variation in the availability of such prey species as capelin and lance and possibly some of the semi-pelagic crustaceans because of hydrographic variation. However, assuming the data collected to represent the average condition the most obvious seasonal difference noted from the stomach contents was the heavy feeding on fish, primarily lance, that were possibly grouping in preparation for late fall or early winter spawning during the late summer and fall in Division 3N (Fig. 5). To the north in Division 3L the biggest intake of fish, principally capelin, occurred during April–June (Fig. 4). Unfortunately no data were available from December to February, in Division 3L or from December to January in Division 3N, however, the March and February samples gave the highest percentage of empty stomachs (Fig. 4 and 5).

Komarova (1939) stated that the maximum feeding of *Hippoglossoides* in the Barents Sea occurred in June–September and was minimal during February–May. Powles (1965) for the southern part of the Gulf of St. Lawrence reported a virtual cessation of feeding during the winter in spite of the fact that the winter and summer temperatures differed very little. MacKinnon (1972a) associated the periods of summer feeding and winter fasting with the annual cycle of energy storage.

The difference in the caloric value of stomach contents for the two areas (Fig. 6) largely reflects the differences in the amounts of fish consumed. In Division 3L plaice stomachs contained fish mainly in the April–June period, but not in such large numbers as in Division 3N during the second half of the year (Fig. 4 and 5), and values calculated for the whole year were higher in the latter area. Added to this was the possible larger amount of energy expended in foraging for echinoderms and molluscs in Division 3L as compared to fish feeding.

An interesting possibility is that the greater consumption of high energy food in Division 3N as opposed to 3L produced the observed earlier maturing (Pitt 1966) and faster growing (Pitt 1967b) fish there. Pitt (1967b) showed a fairly good correlation between the size at age 5 and 15 and the probable bottom temperature with faster growth in Division 3N being related to higher average

TABLE 3. Mean weights of plaice stomach contents for ICNAF Divisions 3L and 3N in transformed units, i.e. 100 (Log weight + 1) by size-groups for seasonal periods. Numbers in parentheses are the total number of fish examined at each size and used to calculate the mean weights.

Period	10–19 cm	20–29 cm	30–39 cm	40–49 cm	50–59 cm	60–69 cm
			ICNAF Division 3L			
March	4.46±0.46 (9)	13.10±4.81 (29)	41.15±11.49 (26)	48.56±11.95 (27)	50.63±17.02 (14)	
Apr.–June	5.01±0.72 (73)	12.16±0.99 (298)	27.20± 1.47 (454)	53.71± 2.60 (425)	65.05± 3.73 (250)	81.30±10.50 (39)
July–Sept.	3.98±1.17 (11)	8.88±1.45 (66)	18.96± 2.32 (86)	41.40± 4.22 (82)	53.15± 8.47 (38)	98.41± 6.51 (4)
Oct. and Nov.	6.02±2.00 (16)	7.75±1.53 (53)	25.63± 4.15 (65)	30.42± 5.99 (61)	44.69± 9.61 (32)	62.44±16.44 (3)
			ICNAF Division 3N			
Feb.	7.92 (1)	4.49±2.87 (20)	6.59± 2.43 (35)	16.74± 4.90 (45)	15.57± 8.62 (21)	30.10±13.10 (3)
Apr.–June	1.38±0.59 (12)	13.96±1.26 (198)	28.93± 1.81 (340)	53.10± 2.77 (318)	78.30± 5.04 (163)	84.14± 9.79 (38)
July–Sept.	3.93±2.08 (5)	12.42±3.26 (57)	33.30± 4.78 (85)	49.91± 6.21 (99)	81.04±10.24 (51)	85.37±17.67 (18)
Oct. and Nov.	nil (6)	24.23±2.05 (209)	58.99± 2.55 (401)	97.32± 3.06 (445)	118.02± 4.86 (241)	133.78±13.06 (38)

temperature than in 3L and McKenzie (1934 and 1935) and Kohler (1964) suggested that, for cod, temperature was related indirectly to growth inasmuch as it controlled food consumption. MacKinnon (1972b), however, found no significant difference between the standard metabolic rates of American plaice at temperatures 1 and 6 C. Low temperatures may, however, reduce the feeding rate because of a reduction in the rate of digestion. Rae (1965), for the lemon sole (*Microstomus kitt*), concluded that the quantity and the type of available food was the major reason for the difference between areas in the rate of growth, and Martin (1952) found that fish-feeding lake trout in Algonquin Park, Ontario, matured earlier and grew faster than the plankton feeders. However, further speculation on the relation between food and growth is beyond the scope of this paper.

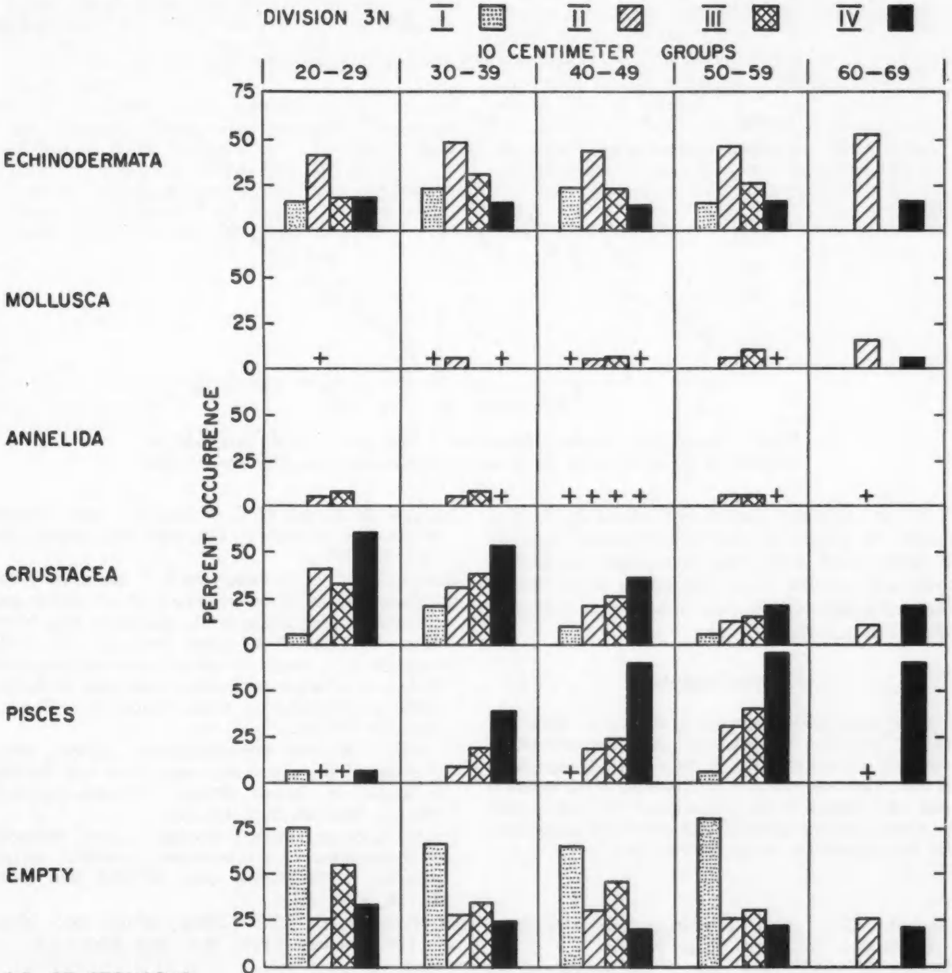

FIG. 5. Seasonal differences in food occurrence for ICNAF Division 3N. (I = February, II = April–June, III = July–September, IV = October and November.) Percentages were not calculated for less than 15 fish. (+)

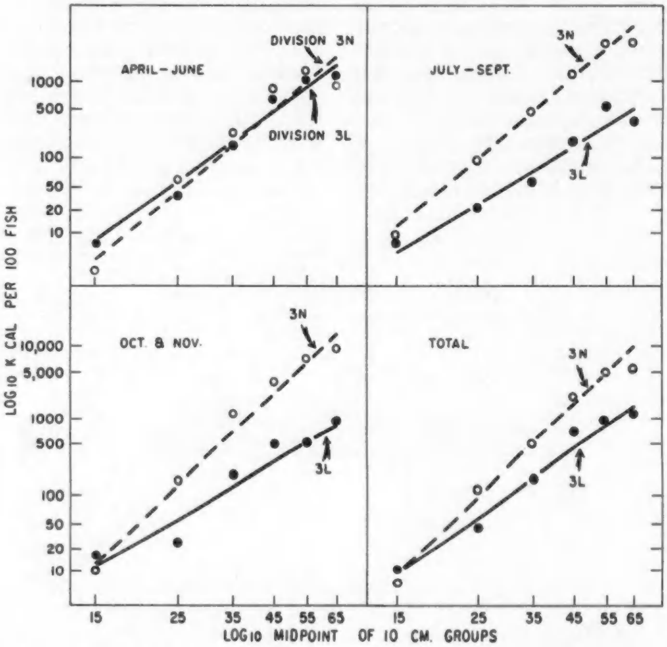

FIG. 6. Unweighted log–log regressions of kcal per 100 fish examined on midpoint or length-group for the monthly periods shown and also annual totals.

To get a complete picture of the food and feeding habits of plaice on the Grand Bank, monthly samples which would fully document the feeding cycle are required. Also required is some idea of the availability of the prey species in relation to what was actually selected.

Acknowledgments

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Two Mechanisms That Make it Impossible to Maintain Peak-Period Yields From Stocks of Pacific Salmon and Other Fishes

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RICKER, W. E. 1973. Two mechanisms that make it impossible to maintain peak-period yields from stocks of Pacific salmon and other fishes. J. Fish. Res. Board Can. 30: 1275–1286.

"Mechanism 1" has two aspects: catches taken at a given rate of exploitation are greater when rate of exploitation has been increasing than when it has been steady or decreasing; also, the yield taken from the progeny of a spawning of a given size is greater when rate of exploitation has been increasing than when it has been steady or decreasing. "Mechanism 2" is the fact that mixtures of stocks of unequal productivity, when harvested together, produce smaller recruitments than single stocks of the same original size and having the same optimum rate of exploitation. In addition, any fishery for a valuable species is likely to develop beyond the optimum rate of exploitation because there is no easily detectable symptom that the optimum is being passed. When this has happened, maximum sustainable yield (MSY) will not be achieved immediately if the optimum rate is imposed subsequent to a period of overexploitation; rather there will be a gradual approach to MSY that extends over several generations after the optimum rate is established. Both of the two mechanisms above, plus the likelihood of unrecognized overfishing, make for a catch maximum while fishing is still on the increase. For salmon this maximum is likely to be 30–60% greater than the sustainable yield. In addition, unavoidable difficulties of management make for even greater differences between the historical maximum and the mean equilibrium yield that can be achieved in practice. Good annual prediction of recruitment can improve this picture because rate of exploitation can then be adjusted to the quantity of fish available; however this procedure too is much less effective when mixtures of stocks are fished in common, because in general the recruitments to different stocks do not vary in exactly the same way. The phenomena described may also contribute to an historical early maximum of catch in fisheries for species such as cod, being independent of and additional to the maximum caused by "removal of accumulated stock."

RICKER, W. E. 1973. Two mechanisms that make it impossible to maintain peak-period yields from stocks of Pacific salmon and other fishes. J. Fish. Res. Board Can. 30: 1275–1286.

Le "mécanisme 1" offre deux aspects: les prises effectuées à un taux donné d'exploitation sont plus fortes quand le taux d'exploitation est allé en augmentant que lorsqu'il a été stable ou en voie de diminution; de plus, le rendement obtenu à même la progéniture d'une ponte d'un ordre de grandeur donné est plus grand lorsque le taux d'exploitation est allé en augmentant que lorsqu'il a été stable ou en voie de diminution. Le "mécanisme 2" est le fait que des mélanges de stocks d'inégale productivité, lorsque récoltés ensemble, produisent des recrutements plus faibles que des stocks uniques de même grandeur originelle et de même taux optimal d'exploitation. De plus, toute pêcherie d'une espèce de valeur est susceptible de se développer au-delà du taux optimal d'exploitation, car il n'existe pas de symptômes facilement décelables pour indiquer que l'optimum est en train d'être dépassé. Lorsque ceci s'est produit, le maintien constant des prises maximales (MSY) ne sera pas assuré immédiatement, si le taux optimal est imposé après une période de surexploitation; il y aura plutôt une approche graduelle au MSY, couvrant plusieurs générations, après l'établissement du taux optimal. Les deux mécanismes mentionnés, en plus de la probabilité d'une surexploitation passant inapercue, contribuent à un maximum de capture quand la pêche est encore en voie d'augmentation. Pour le saumon, ce maximum a des chances d'être de 30 à 60% plus grand que le rendement constant possible. De plus, des difficultés inévitables d'aménagement sont la cause de différences encore plus grandes entre le maximum historique et le rendement moyen d'équilibre possible en pratique. Une bonne prédiction annuelle du recrutement peut améliorer cette situation, car alors le taux d'exploitation peut être ajusté à la quantité de poissons disponible; cependant, cette procédure est, elle aussi, beaucoup moins efficace quand

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des mélanges de stocks sont pêchés en commun, parce qu'en général le recrutement dans des stocks différents ne varie pas exactement de la même façon. Ces phénomènes peuvent également contribuer à hâter le maximum historique de prise dans des pêches, comme celle de la morue, indépendamment et en surplus du maximum causé par "enlèvement du stock accumulé."

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A puzzling problem of Pacific salmon ecology is this: why do the runs of major river systems, when brought under the best available management, rather consistently fail to produce at levels close to what has generally been expected of them on the basis of their past history? In the case of sockeye, for example, there seem to be only one or two major systems today that are yielding more than half of their peak-period catch, and some yield considerably less.

For Pacific salmon our expectation has generally been that stocks should be able to provide an average sustained yield not too much below the observed maximum — for example, not less than 90% of the mean of the best 10-year sequence. This is in contrast to fisheries for species such as cod (*Gadus morhua*) and halibut (*Hippoglossus*), for which it is well recognized that sustainable yield is likely to be half or less than half of the early maximum. These latter species are available to the fishing gear at several ages, and Baranov (1918) showed that the start of exploitation initiates a "fishing-up period" or "removal of accumulated stock," a time during which the population adjusts its age-structure to the increase in mortality rate. But because Pacific salmon spawn only once, this effect does not apply to them insofar as they are caught in their final year of life, which has been the commonest situation. Exceptions are the present Japanese high-seas catches of sockeye, chum, and chinook salmon (*Oncorhynchus nerka, O. keta, O. tshawytscha*) and the North American ocean troll fishery for chinook salmon, both of which include individuals taken during the year before that in which they would mature. With these two fisheries the initiation or intensification of fishing effort must be accompanied by a fishing-up effect, tending to make the immediate catches greater than subsequent ones. However, the historical maximum of catch for all major salmon runs came long before ocean fishing was significant, so that an explanation for it must be sought outside of the fishing-up phenomenon.

A number of special causes of today's reduced salmon catches have been suggested. Sometimes it is possible to point to physical causes of damage to the runs, and these can be of major importance. However, yields far below the historical maximum are now being taken in localities like Bristol Bay where there has been no appreciable disturbance, or on the Fraser River where the major harmful situation was corrected many years ago. Other possible reasons for reduced yields are mentioned in the discussion below. But before straining too hard to assign the full blame to one or more of these, for each run a preliminary question should first be answered: is it possible that the reduced levels of catch are to an important degree natural and inevitable, a built-in feature of the interaction between the salmon and their fishery?

PREVIOUS WORK

If a salmon fishery comes to exceed its optimum rate of exploitation, then by definition the catch has become, or will soon become, less than what it was previously. If subsequently the rate of exploitation is reduced to and held at the optimum level, then (contrary to an easy expectation) the maximum sustainable yield does not immediately become available; rather, the spawning stock takes a number of generations to recover its optimum abundance (Ricker 1958a, Fig. 11.5, 11.6). In addition, it was found that a maximum of catch somewhat in excess of the maximum sustainable yield can usually be expected during the developmental period of a salmon fishery even if the best equilibrium rate of exploitation is never exceeded. However for single stocks this effect is small quantitatively, and cannot explain anything more than a minor part of the catch maxima actually observed.

This paper extends the earlier analysis by examining the history of utilization when stocks having different productive capacities are harvested in common.

DEFINITIONS

I define a "unit stock" or simply "stock" as a group of salmon that spawn in the same stream or region of a lake, at about the same time of year. It is the smallest aggregate of fish that has even partial genetic individuality. In the case of sockeye, a single nursery lake may support a dozen or more different stocks. A "run" is a mixture of stocks migrating toward or up a river at any particular season.

The "maximum sustainable yield" (MSY or C_s) of a salmon stock is the average number or weight of surplus adult fish produced when its spawners have been reduced to the level of abundance (P_s) at which the mean difference between recruitment (R) and P_s is greatest. Following any long period of no fishing there exists a natural state in which (on the average) recruitment equals the spawning contingent; let the mean number of fish in such spawnings be P_r. The productivity of a stock can then be defined as C_s/P_r, or MSY divided by the replacement abundance of spawners. The optimum rate of exploitation is equal to C_s/R_s or $C_s/(C_s + P_s)$.

Notice that productivity, in this sense, is not directly related to absolute stock size or absolute yield. There can be very productive small stocks, and unproductive large ones.

Single-Stock Model

A convenient and widely used set of simple reproduction curves for salmon stocks are the so-called "Ricker" curves having the formula[1]:

$$\log_e R = \log_e P + a(1 - P/P_r) \qquad (1)$$

The coefficient a can have values from 0 up to an indefinitely large figure, but for salmon it would rarely if ever exceed 3. In using (1) for modelling the most convenient value of P_r is 1, in which event R and P will both be expressed as fractions of the replacement stock (the same is true for the other expressions below).

Recruitments calculated from expression (1) represent geometric mean values of R at given P. Superimposed on this is the variability due to causes other than those associated with the size of the spawning stock.

Parameters Used

The value of the coefficient a for the first stock to be considered is 1.25, and its recruitment curve is shown in Fig. 1. For a realistic picture of the development of a salmon fishery I have used Milne's approximate 5-year-mean rates of exploitation for the Skeena River sockeye fishery from 1870 to 1954 (Table 1). The generation is assumed to be 5 years long. All catches are in terms of the replacement level of stock, the latter being taken as 1000.

Maximum Sustainable Yield

The size of spawning stock (P_s) that will provide maximum sustainable yield (MSY) for a curve described by expression (1) is found by equating its slope to 1. This produces expression (2), which can be solved for P_s by trial (putting $P_r = 1$):

$$\log_e(1 - aP_s/P_r) + a(1 - P_s/P_r) = 0 \qquad (2)$$

From the P_s so obtained the corresponding recruitment (R_s) can be calculated from (1), hence MSY $= C_s = R_s - P_s$, and optimum rate of exploitation $= u_s = C_s/R_s$. For $a = 1.25$, $u_s = 0.52$.

Catch Sequence

In what follows, catches, recruitments, and spawning stocks are all given in terms of a replacement stock of 1000. Starting from the first years of the fishery, the

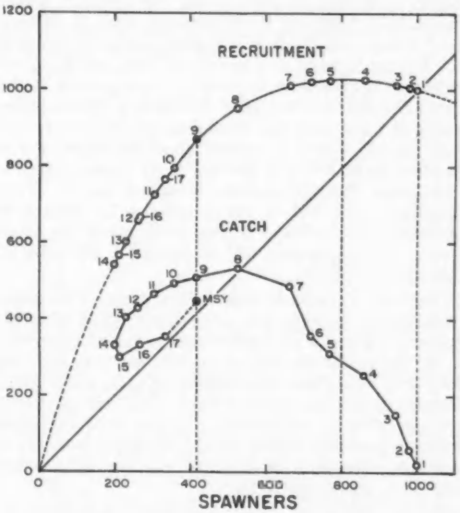

FIG. 1. Progress of catch and recruitment for a single stock, when subjected to the succession of exploitation rates in Table 1. Recruitment and catch are plotted against the spawning stock that produced them, and generations are numbered in sequence. The upper curve is the recruitment curve for $a = 1.25$ in expression (1).

TABLE 1. Sequence of estimated rates of exploitation in the Skeena sockeye fishery, averaged by 5-year generations starting in 1870–74. (From Ricker 1958a, table 11.3, after Milne 1955.)

Generation	Rate of exploitation	Generation	Rate of exploitation	Generation	Rate of exploitation
1	0.02	7	0.48	13	0.67
2	0.06	8	0.56	14	0.61
3	0.15	9	0.59	15	0.53
4	0.25	10	0.62	16	0.50
5	0.30	11	0.64	17	0.46
6	0.35	12	0.65		

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[1] The derivation of expressions (1)–(6) is summarized in publications by Ricker (1958a, 1971, 1973), among others.

catch removed in successive generations is shown as Stock 3 in the lower panel of Fig. 2. Figure 1 shows recruitments and catches plotted against the spawning stock of each generation. The size of successive new broods of recruits increases somewhat at first, then falls off, following the line of the recruitment curve. The catch reaches a maximum at 533 in the 8th generation, then decreases as rate of exploitation continues to increase.

At generation 14 exploitation starts to decrease again, and in the following generation the recruitment begins to ascend the same curve. The catch, however, moves to a new and lower position (Fig. 1). Why is this? During the phase of increasing rate of exploitation (*u*), the catch taken at a given *u* is from the larger recruitment produced by the larger spawning stock of the parental generation just past. But when *u* is decreasing, the catch for a given *u* is taken from the smaller recruitment provided by the smaller spawning stock of the parental generation just past[2] (Fig. 3). Turned around, this means that the recruits produced by any given spawning stock will be fished less heavily when *u* is decreasing than when *u* is increasing, hence the catch from a given spawning will be smaller. I will refer to this as "Mechanism 1".

The level of equilibrium catch for a given *u* is naturally intermediate between the catch taken when *u* is increasing and that when *u* is decreasing. If after generation 17 of the model the rate of exploitation is brought to 52% and kept there, the recruitment after a few generations reaches its optimum value (862) and the catch reaches MSY at 447 (Fig. 1, 3). The time from the start of decreased fishing to the optimum position is about 6 generations, or 30 years. The maximum catch was 19% greater than MSY.

CATCH SEQUENCE IF THE BEST RATE OF EXPLOITATION IS NOT EXCEEDED

If in Fig. 1 the best rate of exploitation u_s had never been exceeded, it would mean moving from 48% exploitation at generation 7 to 52% at generation 8, and staying at that level. The catch then moves asymptotically toward the MSY position, getting within 2% of it after 3 generations, while the recruitment similarly approaches the MSY position along the recruitment curve. In this sequence the maximum catch differs from MSY by only 10%. The size of this difference of course depends on how rapidly MSY is approached. The limiting case would be where 52% exploitation was initiated at the start of the fishery, giving a first and largest catch of 520, 16% above MSY.

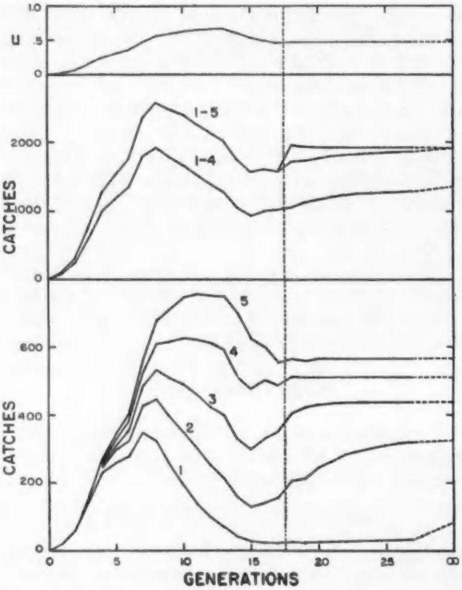

FIG. 2. Catches in successive generations for the individual stocks of Table 2 and for two combinations. The replacement abundance of each stock is 1000. *Top panel*: rates of exploitation from Table 1. *Middle panel*: total catch from Stocks 1–5 and from Stocks 1–4. From generation 18 onward exploitation is stabilized at 54 and 47% for Stocks 1–5, and at 44% for Stocks 1–4. *Lower panel*: catches from the individual stocks. From generation 18 onward exploitation is stabilized at 47% for all stocks.

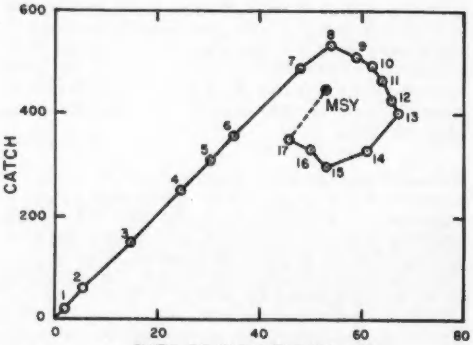

FIG. 3. Catch taken in successive generations from the single stock of Fig. 1, plotted against the rate of exploitation that prevailed during the catch year.

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[2] These statements are true only to the left on the dome of the recruitment curve. However, it is practically impossible that a trend toward decreasing rate of exploitation would start to the right of a dome, although in earlier years there was a tendency for the exploitation in years of an abundance of fish to be less than in adjacent poorer years, because of saturation of canning capacity or of markets.

Models of Mixed Stocks

All major runs of salmon consist of a number of separate stocks whose spawning sites or times are different, and which may differ in various other ways such as rate of growth, length of freshwater life, and so on. Most important here are their differences in productivity (in the sense defined earlier), which implies a difference in the shape of their reproduction curves. Ideally it would be desirable to harvest each stock separately so that each could be given the rate of exploitation needed for its own best yield. To some extent selective harvesting is possible, but in every large river there are stocks that are so thoroughly mixed in the fishing areas that to a large extent they must be fished together.

Paulik et al. (1967) have considered the situation where two or more stocks having different productivities are harvested by the same fishery, but they deal only with equilibrium situations. Here we are more concerned with the historical sequence of catches.

PARAMETERS USED

The principal model to be used consists of a mixture of five stocks fished in common, all of which were of the same abundance at the time fishing first began. All the stocks are characterized by recruitment curves described by expression (1); their coefficients are $a = 0.7, 1, 1.25, 1.5$, and 1.75, respectively. Key numerical values for each curve are shown in Table 2. For $a = 1$ recruitment is a maximum at the replacement level (P_r). For $a > 1$ maximum recruitment is at values of P less than P_r, so that there is a dome of the curve to the left of the replacement point, as in Fig. 1. For $a < 1$ the curve is monotonic to the left of P_r and has its maximum to the right of it. Thus, large a means a productive stock, and small a an unproductive one (for examples see fig. 11.2 of Ricker 1958a).

MAXIMUM SUSTAINABLE YIELD

For a mixture of stocks there is no simple expression for the combined optimum rate of exploitation, so it is necessary to use trial and error. For any given equilibrium rate of exploitation (u_E) the size of spawning stock (P_E) can be found that produces the equilibrium catch for that u_E, as follows:

$$\frac{P_E}{P_r} = 1 + \frac{\log_e(1 - u_E)}{a} \qquad (3)$$

From each calculated P_E the corresponding recruitment R_E is computed from (1), and the sustainable catch is $C_E = R_E - P_E$. Values of C_E were calculated from a series of values of u_E for each of the five stocks above, and the catches for each u_E were summed to obtain the total picture when all stocks are fished in common, as shown in the upper panel of Fig. 4.

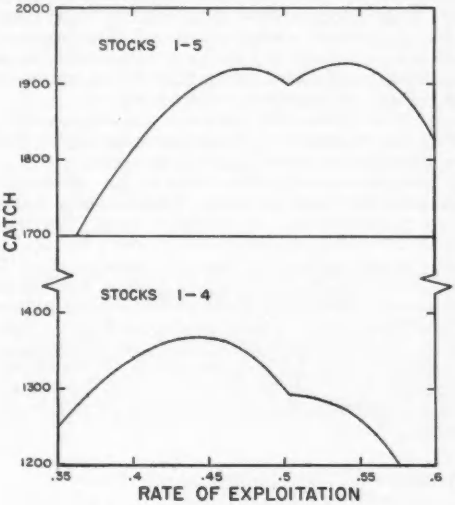

FIG. 4. Sum of equilibrium catches plotted against equilibrium rate of exploitation (u_E) for recruitment curves 1–5 (top panel) and 1–4 (bottom panel).

TABLE 2. Characteristic statistics for the recruitment curves used. The replacement level of stock in each case is $P_r = 1000$.

Stock no.	1	2	3	4	5
Parameter a	0.7	1	1.25	1.5	1.75
Maximum recruitment (R_m)	1058	1000	1027	1102	1210
Spawners needed for maximum recruitment (P_m)	1429	1000	800	667	571
Maximum sustainable yield (C_s)	211	330	447	587	745
Spawners required for MSY (P_s)	454	433	415	397	379
Recruitment at MSY (R_s)	665	763	862	984	1124
Rate of exploitation at MSY (u_s)	0.317	0.433	0.519	0.596	0.662
Limiting equilibrium rate of exploitation (u_E(max))	0.503	0.632	0.714	0.777	0.826

The best overall rate of exploitation lies in the region between 0.4 and 0.6. In this region there happen to be two maxima, at 0.47 and 0.54. The sustainable yields they provide are 1919 and 1926, respectively — practically the same (this of course is accidental). At $u_E = 0.54$ Stock 1 is gradually eliminated from the fishery, and the notch near $u_E = 0.50$ in Fig. 4 reflects this disappearance.

Catch History

Again using the rates of exploitation of Table 1, recruitments and catches for each of the five curves above were computed, then summed to give the overall picture (Fig. 2). With this sequence there is a catch maximum at 2590 in the 8th generation of the fishery. This is followed by a decline in catch that continues to the end of the expansion period and persists for 2 generations after exploitation starts to slack off. The minimum catch is 1559, about 60% of the maximum, after which it changes little for 2 generations during which the exploitation rate continues to decrease.

As noted above, the maximum sustainable yield is 1926, or 664 less than the historical maximum; that is, the maximum was 35% greater than MSY.

Naturally the individual stocks in this exploitation sequence fare very differently (Fig. 2). Stock 1, the least productive one, is reduced to a very low level — in the last (17th) generation its catch is only 22. In the same generation Stock 2 produced only 155, about half the potential yield, and Stock 3 produced about four fifths of its potential yield. For both of these the 47% rate of exploitation was not far from the optimum (Table 2), but neither stock had yet recovered completely from the previous interval of overfishing. Stocks 4 and 5, on the other hand, were both below their maximum sustainable yields because of not enough fishing.

Approach to Maximum Sustainable Yield

From generation 18 onward Fig. 2 shows the sequence of catches if each of the five stocks were to be exploited at $u = 0.47$, the lower of the two optimum rates. It takes some time for the equilibrium point to be reached, especially for Stock 1. For practical purposes (within 5%) the maximum combined catch is reached by generation 22. This is 5 generations after the optimum rate of exploitation was introduced, which means it took 25 years to achieve MSY. From the time of the first reduction in rate of exploitation in generation 14 there are 4 generations more, or 45 years in all. If 90% of MSY be considered sastifactory, this is achieved in generation 20, or 35 years after fishing pressure began to be relaxed. Evidently the effects of a period of overfishing may persist for a considerable length of time after it has been corrected.

If the equilibrium at 54% exploitation is chosen, MSY is achieved at once in generation 18 (20 years after the first restriction of fishing); in fact there is a slight temporary excess (Fig. 2). On balance, however, the preferable management procedure would be to use $u = 0.47$, for three reasons: (1) at 47% a larger spawning stock is available, and this will be better able to withstand and overcome any of the natural or accidental misfortunes that occur from time to time; (2) no stock is exterminated, so that more options exist for future manipulation: for example, it might be possible to increase the productivity of Stock 1 by improvements to its spawning grounds; (3) a larger spawning stock gives a greater "cushion" in case MSY has been estimated too high.

Catch Sequence if the Best Rate of Exploitation is Not Exceeded

Suppose the smaller optimum exploitation rate of 47% were never exceeded, which means stabilizing the fishery at that level in generation 7. In that event the catch maximum would occur in the 7th generation instead of the 8th, and would be smaller — 2315 instead of 2590, but still 20% greater than the MSY of 1921. If stabilization occurred at the other best exploitation rate, 54%, starting in the 8th generation, the maximum catch of 2500 would be taken in that generation and would be 30% greater than MSY. The corresponding figure for the single stock was 10%.

For the limiting case where the fishery begins at an optimum equilibrium rate of exploitation and stays there, the initial catch would be either 2350 or 2700, respectively, 22 and 41% above MSY. The corresponding figure for the single stock was 16%.

Pattern of Change in Recruitment

Figure 5 shows the succession of recruitments and catches for the five stocks combined, plotted against spawning populations. The obvious difference between Fig. 1 and Fig. 5 is in the line showing successive recruitments. When rate of exploitation starts to decrease, the single stock of Fig. 1 retreats upward along the same recruitment curve as it followed during the increasing phase. *With the mixture of stocks the journey back is along a lower line.* In our model the decreasing phase is taken only as far as $u = 0.46$ in generation 17, but if a gradual decrease in exploitation were to continue there would be a complete lower line that would eventually return to the starting point of 5000 stock units.

Moreover, even the equilibrium level of recruitment is less than the recruitments obtained during the phase of increasing exploitation, as illustrated by the upper pair of black dots in Fig. 5. As for why this should be, the simplest answer is that it works out that way; it is not anything that I had anticipated. However, in the lower panel of Fig. 2 notice that Stocks 1–5 all start out with the same contingent of spawners (1000), whereas at equilibrium for $u = 47\%$ their spawners are about equal to the catches indicated on the right-hand ordinate. To bring Stock 1 from 1000 down to an equilibrium level of 80 a large body of fish had to disappear, and this accounts for most of the difference between the recruitments in the upper line of Fig. 5 and the equilibrium positions below it.

This difference between the combined recruitments from mixtures of stocks, depending on whether rate

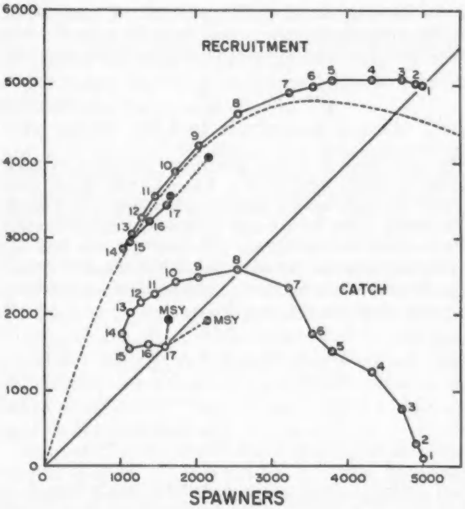

FIG. 5. Progress of catch and recruitment for the combination of Stocks 1–5, when subjected to the exploitation rates of Table 1. The broken curve is a "Ricker" curve fitted to the recruits actually obtained in generations 8–17.

of exploitation has been increasing, decreasing, or staying steady, will be referred to as "Mechanism 2."

SEQUENCE OF CATCHES

Comparison of Fig. 1 with Fig. 5 also indicates a general similarity of the two catch sequences up to the time that rate of exploitation begins to decline. But during generations 15–17 the difference between the catches of the increasing and the decreasing exploitation episodes becomes greater for the mixed stocks than for the single stock. This increased contrast is a result of the smaller recruitments obtained from a given spawning (Mechanism 2).

SINGLE-STOCK APPROXIMATION TO A MULTIPLE-STOCK SITUATION

Another feature of the combined recruitment line of Fig. 5 is that it does not correspond exactly to any single curve of the type of expression (1). However, if such a curve is fitted as an approximation, it will usually be a good enough guide to the optimum rate of exploitation. Information on catches, and particularly on recruitments, for the earlier stages of a fishery will commonly be lacking or of poor quality, and the original mean abundance of the run will be unknown. In Fig. 5 the broken curved line is a Ricker recruitment curve fitted to the data for generations 8–17. The value of a is 1.273; the replacement stock is 930 instead of 1000; and the optimum rate of exploitation is 0.52, intermediate between the two actual values (0.47 and 0.54). Thus although the original stock is estimated 7% too low, the exploitation rate indicated lies between the two optima and would give almost the maximum sustainable yield.

The fitted curve also describes quite well the history of the catch up to the time of its minimum. Figure 6 shows the sequence of catches computed from the curve of $a = 1.273$ and the rates of exploitation of Table 1, as compared with the actual catches. The two series were brought to a common basis by equating their total catches of generations 8–17, the initial abundance being taken as 10,000. The computed catches are only very slightly less than the actual catches up to the time the catch reaches its minimum in generation 15. Beyond that point, however, the single-stock model predicts catches greater than the actual during the restoration phase (generations 16 and 17). Subsequently, if at generation 18 and onward the fishery is stabilized at the optimum rate (52%) suggested by the fitted curve, the projected sustainable yield is 4360; whereas if the actual mixture of five stocks is fished at that rate the equilibrium yield is only 3836.

Thus the single-stock model overestimates the yield potential of the run by 14%. This exact figure is of course not unique. If a longer or shorter series of P and R values is used to fit the curve, the difference can be either greater or less.

Relation Between Range of Productivities and Rates of Exploitation

Obviously an indefinitely large number of combinations of sequences of exploitation and mixtures of stocks can exist in theory. To examine even a small part of the possibilities at random would be a protracted task, and not a particularly rewarding one. I have there-

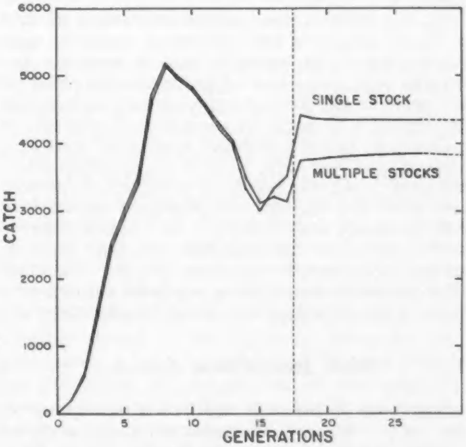

FIG. 6. Comparison of the catches taken from Stocks 1–5 with those indicated by a fitted curve (broken curve of Fig. 5).

fore considered a known sequence of exploitation rates and a simple set of associated reproduction curves that produces a catch sequence and optimum rate of exploitation similar to the actual situation on the Skeena River.

A variant of this set was also examined: a combination of Stocks 1–4 of Table 2. Figure 4 shows that in this case there is a unique best rate of exploitation at 44%. Figure 2 indicates that the catch sequence is similar to the 5-stock series, with a maximum in generation 8 and a minimum in generation 15, but the difference between these extremes is greater: the maximum is more than twice the minimum, and is 41% greater than the maximum sustainable yield. If the 4-stock series is maintained at its best exploitation rate of 44% after generation 17, it reaches MSY (within 5%) only after 14 more generations, or 18 generations (90 years) after rate of exploitation began to decrease. The reason for the long recovery period is that Stock 1 had been fished down close to extinction and Stock 2 was also much reduced, so their rehabilitation in the face of an active fishery is a protracted process.

In some respects the 4-stock model is a better representation of the actual Skeena catch sequence than the 5-stock: the maximum 5-year mean catch in the sequence starting 1905 is 2.05 times the minimum, and for the model it is 2.09. However the actual time interval between maximum and minimum was 25 years, whereas in the model it is 35 years.

If a mixture of stocks having considerably greater productivities than Stocks 1–4 or 1–5 were to be combined with the fishing sequence of Table 1, there would be no period of overexploitation. The phase of decreasing rate of exploitation would then represent an irrational retreat to underutilization, which would of course be very unlikely to occur. Thus, practical considerations set limits to the kinds of combinations that have actually existed.

What is likely to have happened for almost all runs of Pacific salmon is that exploitation sooner or later came to exceed the level that provides maximum sustainable yield, no matter what the absolute value of this optimum rate for each particular run. Both in Asia and in North America, for most runs of most species the optimum rate of exploitation was reached some time between 1890 and 1930, when biological information, if it existed at all, was insufficient to identify an optimum rate. When the optimum was passed the catches were still increasing, and there were no obvious signs of trouble ahead. At the same time the high value of salmon as compared with other fish, and the small effort required to harvest them, precluded any economic brake on the upward trend in rate of fishing at this stage.

Other Recruitment Curves

Expression (1) has been used here as a convenience, but many other sets of mathematical or empirical relations would be just as good and would reveal a similar picture. It is necessary only that there be a mixture of stocks whose optimum rates of exploitation are sufficiently different.

As an example of a different type of recruitment, similar computations have been made for a set of curves described by the Beverton–Holt hyperbolic formula:

$$R = \frac{P}{1 - A\,(1 - P/P_r)} \qquad (4)$$

The new symbol A is a parameter having a possible range of values from 0 to 1. These curves differ from (1) in that they have a positive asymptote which is the maximum value of R, and recruitment never exceeds the replacement level when spawners are less than P_r; some examples are shown in fig. A2 of Ricker (1958a). For this set of curves the expressions corresponding to (2) and (3) above are, respectively:

$$\frac{P_s}{P_r} = \frac{A - 1 + \sqrt{1 - A}}{A} \qquad (5)$$

$$\frac{P_E}{P_r} = 1 - \frac{u_E}{A} \qquad (6)$$

The mixture of four originally-equal stocks having A = 0.3, 0.6, 0.8, and 0.9 was computed to have a best equilibrium rate of exploitation of 50%. At this rate the least productive stock (A = 0.3) will have disappeared; to save it in viable numbers exploitation would have to be reduced to about 25%, at which level the equilibrium yield would be 27% less than MSY.

Combining these four stocks with the exploitation sequence of Table 1 gives the following picture (P_r = 4000);

	Generation	Magnitude
Maximum catch	8	1473
Minimum catch	15	800
Maximum sustainable yield	–	986

MSY is obtained from 1972 recruits produced by 986 spawners, the latter being slightly less than a quarter of the primitive level of abundance.

The sequence of catches obtained is very similar to that for the four stocks from the Ricker curve (Fig. 2), except that in the Beverton-Holt situation the absolute level of yield (relative to the unexploited level of abundance) is considerably less at all stages. The maximum catch is 84% greater than the minimum, and is 49% greater than MSY. If the optimum level of exploitation (50%) is introduced in generation 18 and maintained thereafter, the catch will be within 5% of MSY in generation 22, which is 9 generations (45 years) after the rate of exploitation began to decrease.

Discussion

1. The mixtures of stocks used above, and others that have been examined, display the same yield characteristics as single stocks but in an exaggerated form. For the single stock of Fig. 1 the sustainable catch is 90% of the maximum.

For stocks 1–5 of Fig. 5 this figure is 74%. Thus the mixtures arouse greater expectations, relative to actual sustainable performance, than does a single stock having a similar optimum rate of exploitation.

In general, the more unproductive stocks there are in a mixture, the lower the sustainable yield will be relative to initial abundance, and the lower it will be relative to the historical catch maximum. The ranges of productivities used in this paper do not at all represent the possible extremes. It is the nature of animals, of whatever sort, to penetrate into every habitat where they can eke out a living. Hence it is to be expected that there once existed salmon stocks (even fairly large ones) in marginal situations that needed almost the whole of their recruitment for spawning in order to survive. In terms of equations (1) or (4) this means a value of a or A approaching zero.

Such stocks would disappear during the developmental period of the fishery. On the spawning grounds this disappearance would scarcely be noticed amid the general abundance of breeding fish in those days (mostly before 1900), when in any event the information available was poor or lacking. While they lasted, however, such stocks may have contributed importantly to the large runs and easy catches that were then available in the commercial fishing areas. On the other hand, some sockeye stocks are known that have withstood exploitation rates of 80% or more for many years (though not at MSY). This implies that $a>1.6$ or so in expression (1), or $A>0.8$ in expression (4).

On the whole, therefore, we should expect the maximum sustained yield from a mixture of stocks to be no more than 80 to 85% of the historical maximum. The lower limit for MSY might be in the region of 60% of the maximum provided no originally-large stocks are exterminated, but if extermination occurs there is no theoretical lower limit. The 4- and 5-stock Ricker models above give maximum sustained yields that are 71% and 74% of the historical maximum, while for the Beverton-Holt model the figure is 67%. In any event our greatest skill in regulating fishing on mixed stocks can never bring the sustainable yield back close to its historical peak performance.

2. For sockeye and (probably) pink salmon the recruitment picture can be complicated by interaction between the different year-classes (Ricker 1950, 1962, Ward and Larkin 1964, Larkin 1971). If one age of maturity predominates, such interaction causes the phenomenon of dominant lines or "cycles." In such circumstances an ordinary reproduction curve based on points for individual years will not be useful for estimating maximum sustainable yield. The dominant year-classes will be the largest and will exhibit the greatest spread between R and P, but their continued existence requires that less productive year-classes be present. Hence the level of sustainable yield that they indicate will be the maximum, but it will not be attainable every year: more likely in only 1 or 2 years out of 4 or 5 for sockeye, or every second year for pinks.

The mechanism of interaction can work in either direction. Fish of the dominant line may directly suppress the "off" line or lines, for example by cannibalism, which is a possibility in the case of pink salmon (*Oncorhynchus gorbuscha*). Alternatively, the small lines may make possible the existence of the dominant line by periodically reducing a set of predators or parasites to a low level of abundance, e.g. the trout in a sockeye lake, as suggested by Ward and Larkin's (1964) work at Shuswap Lake.

The fact of interaction, and its consequences, need not even be limited to situations where "cycles" exist. A regular sequence of dominant lines cannot persist when the fish mature at two or more ages in more or less equal numbers, as with northern sockeye, but it may still be true that exceptionally large recruitments from moderately large spawning stocks imply the preceding or subsequent existence of year-classes of much smaller productivity.

These complications can be countered, to a first approximation, by using figures for catch and fishing effort averaged over the length of a generation. Our models are based on an exploitation sequence for sockeye, so 5-year averages were used because female sockeye mature mainly at 4–6 years of age.

3. Insofar as two or more stocks occupy the same limited environment at some stage of their life history and compete for food or space, reduction of the abundance of a less productive stock may permit a more productive one to increase. This could, for example, soften the unfavorable effect of overexploitation when it occurred. Such interaction is most likely to exist among sockeye stocks that use the same lake for their year or two of freshwater life, or among stocks of cohoes (*Oncorhynchus kisutch*) using the same stream. In a lake the quantitative aspects of such interaction presumably depend on the degree to which the food production is being utilized, and on how serious are the effects of competition at this stage on survival to the adult stage. In a stream, space might be more important than food.

4. In the analysis above the historical beginning of fishing is to be interpreted as the start of the commercial fishery. Most salmon runs were of

course fished by subsistence fisheries long before commercial utilization began. The stocks are assumed to have reached some sort of equilibrium with the subsistence fisheries, which in effect are considered as part of the natural mortality.

5. As mentioned earlier, the numerical value of the ratio of the historical maximum of catch to a subsequent minimum depends a great deal on the actual sequence of rates of exploitation that happens to prevail. Apart from major physical catastrophes and the effects of Mechanisms 1 and 2 above, the minimum level of catch that followed the maximum in any salmon fishery depended on how much and for how long exploitation had been allowed to exceed the optimum level. In this respect the series of Table 1 is not at all extreme. The reduction in effort at generations 14 and 15 was partly a slow response to the economic depression of the 1930s and, more particularly, a result of special circumstances during the early war years. Without these, rate of fishing might have stayed near its maximum level for 10 years or so longer, after which scarcity of fish would have forced a retrenchment.

In the catch sequence of Fig. 2 the principal cause of the minimum of catch at generation 15 is the interval of overfishing during generations 8–14. However, it is well to remember that there would have been a smaller catch maximum even if the optimum rate of exploitation had never been exceeded. Such a maximum is larger for mixtures of stocks than for a single stock having the same optimum rate of exploitation as the mixture.

6. The models above have compared catches taken by maximum and optimum rate of exploitation, with a tacit assumption that the latter is obtainable. In practice, whereas no special effort or skill is required to reach a maximum, rather precise management is needed to achieve the optimum, and for numerous reasons management must always be something less than perfect from the MSY point of view. To mention only one such factor, "hardship" considerations may make it necessary to take more than the optimum number of fish in a given year, even at the cost of reduced supplies in future years.

However, the manager has an advantage that alleviates his difficulties somewhat. The figures above show ratios of recruitments to spawners (R/P) obtained by computation from the mean curves under average environmental conditions, whereas actually there is much year-to-year variability in this ratio at any given P. Ricker (1958b) showed that environmentally caused variability in recruitment changes the long-term average harvest very little if the same best mean rate of exploitation is used in all years. However, such variability offers an opportunity for a moderate increase in this average harvest, obtained by adjusting the amount of fishing according to some strategy related to the recruitment actually obtained in each individual year. This has been demonstrated for single stocks by Ricker (1958b), Larkin and Ricker (1964) and Allen (1973), using a variety of strategies. For mixed stocks the same opportunity exists, although in a considerably diluted form because only part of the variability in R at given P is determined by causes that affect all the stocks in a run similarly. Nevertheless the opportunity for improving overall yield is quite real, whenever any fairly good estimate of the fish available can be obtained either before fishing starts or early in the run.

In this connection, it is fortunate that the curves of yield against equilibrium rate of exploitation, such as Fig. 4 above, are rather flat near the maximum. For the 5-stock mixture, for example, any rate of exploitation between $u = 40\%$ and $u = 60\%$ will provide not less than 94% of the maximum sustainable yield. Furthermore, if too few fish are caught in a given year within this range of u, an almost equivalent extra number should be available in the next generation; or if too many are caught, they, plus a few extra, can be deducted from the catch to be taken from the next brood and there will be no continuing damage. However if the number of spawners is off target by 25% or more, in either direction, the long-term reduction in yield begins to become important.

7. Various possible causes of a decline in the yield of salmon runs have been observed or suggested. Apart from obvious hazards such as slides, dams, irrigation diversions, and continuing overexploitation, these include: (a) decrease in the fertility of freshwater nursery areas because of the unavoidable reduction of the spawning stocks entering them (applies especially to sockeye); (b) deterioration of spawning success because of silting, scouring or change in flow regimes, due to logging, agriculture, or other human activity; (c) deterioration of ocean survival rates because of climatic change or because of the increase in abundance of fur seals from 1910 to 1950; (d) cumulative hereditary decrease in the ocean growth rate of salmon because of selectivity in harvesting (the larger fish of a given age being more vulnerable or more sought after, so that the smaller ones contribute more to reproduction); (e) cumulative hereditary decrease in mean age at maturity for the same reason as above, and more particularly because longer-lived fish are vulnerable to some types of fishing at more than one age (the latter

applies especially to chinooks); (f) if a run begins to be harvested in the ocean some time before the fish are completely grown, the total yield is reduced because these fish are caught at a time when growth rate will exceed natural mortality rate during the rest of their ocean life.

These and other possible factors can be discussed usefully only in relation to a specific stock or run. But before deciding how much decline in yield needs to be explained in some such manner, for each individual run an attempt should be made to evaluate its history and current position simply from the standpoint of the effects of the fishery on a mixture of stocks of different inherent productivities.

8. If even the best regulation of the fishery cannot provide the catches we have expected, it is natural to look to artificial measures for increasing productivity. This development is already under way for some runs. Its theoretical aspects, although reasonably simple, do not appear to have received any detailed exposition. Here we need notice only that, when there is a common fishery, measures for increasing productivity will be most useful if they are focussed on stocks of lower than average productivity, so as to bring them up to the average or somewhat above it. Most efficient utilization of a mixture of stocks is obtained when all have approximately the same optimum rate of exploitation. The opposite plan, of making one or two of the most productive stocks produce still more, is to a considerable extent self-defeating, as Paulik et al. (1967) have emphasized. If the overall rate of exploitation is increased so as to harvest the greater surplus made available from these stocks, then at the new equilibrium the catch from most of the remaining stocks in the common fishery will become less. The result may be very little overall net increase in sustainable yield, possibly even a net loss.

9. The effects discussed in this paper need not apply only to Pacific salmon stocks. Mechanism 1 should apply to all fisheries, insofar as the phase of increasing rate of exploitation occupied more than the length of a generation. Mechanism 2 seems applicable to any fishery that operates on a mixture of stocks of different productivities, such that the less productive ones may be greatly reduced or even eliminated as fishing is intensified. For species like cod or herring these would be additional causes of a maximum of catch during the phase of increasing rate of exploitation, having results similar to but independent of the well-known fishing-up effect. In practice it would be extremely difficult to separate fishing-up from the postulated effects of the two mechanisms above, in catch statistics. As regards Mechanism 2, however, any abandonment of local spawning areas, such as has occurred in certain herring regions, might be an indication of the disappearance of less productive stocks.

10. Finally, Mechanism 2 can also play a role when mixtures of species are fished together, something that is common in trap and trawl fisheries, especially in the warmer waters of the world. Even in cool regions there have been histories of sequences of species predominating at successive stages of a fishery, a classic example being the flounders of the Bay of Peter the Great as described by Moiseev (1953). Similarly in the history of fish catches from the North American Great Lakes, especially Lake Erie, there are sequences that might be explainable as the replacement of species of less productivity by species of greater productivity when subjected to a common fishery.

Summary

1. The *productivity* of a unit stock is defined as its maximum surplus production or maximum sustainable yield, in numbers, divided by its primitive abundance. This definition is applicable in terms of weight also, in the case of species for which each individual is exposed to capture only during its final year of life, as is true of many stocks of Pacific salmon.

2. The *catch* taken from the recruits produced by a given size of parental stock of salmon is greater when rate of exploitation (u) is increasing than when it has been steady or (still more) when it has been decreasing (Fig. 1). Equally, the catch taken by a given u is greater when u has been increasing than when u has been steady or decreasing (Fig. 3). This is called "Mechanism 1", and it applies either to single stocks or to mixtures of stocks.

3. The *recruitment* per spawner produced by a mixture of stocks of different productivities is greater when exploitation has been increasing than when it has been steady or (still more) when it has been decreasing (Fig. 5). This is called "Mechanism 2"; it is independent of and (in its effect on catch) is additional to Mechanism 1.

4. As a result of Mechanism 2, when combinations of stocks of different productivities are fished in common, they provide a smaller maximum sustainable yield than a single stock of the same initial abundance and having the same optimum rate of exploitation.

5. Even without overexploitation there is a maximum of catch during the developmental period of a salmon fishery. For single stocks this will rarely be more than 15% above the maximum sustainable yield, and usually less; for mixtures of

stocks such a maximum can easily be 20–30% greater than MSY.

6. If the level of fishing for a salmon run increases into the overexploitation range for several generations, after which the optimum rate of exploitation is adopted, it will be several to many additional generations before maximum sustainable yield is achieved.

7. Since there were no obvious signs to indicate when the optimum rate of exploitation had been reached, in all probability most salmon fisheries sooner or later experienced at least a moderate degree of overexploitation.

8. Combining moderate overexploitation with Mechanisms 1 and 2 above, the historical maximum of catch in a salmon fishery can easily have been twice as great as the maximum sustainable yield, and was probably rarely less than 1.5 times MSY, depending on the mixture of stocks being fished and the actual sequence of exploitation rates that occurred. In this way the history of the catches taken from a run has aroused expectations that cannot be satisfied by even the best present regulation of the fishery.

9. If a multiple-stock fishery is fitted by the reproduction curve for a single stock, the latter may predict the best rate of fishing quite well, but the level of maximum sustainable yield is somewhat overestimated — probably by 10–20%.

10. The above effects are additional to any reduction in productivity ascribable to overt causes such as dams, diversions and premature harvesting, or to the less obvious effects of environmental or genetic deterioration.

11. This situation emphasizes the desirability of active intervention to increase productivity. However for good results this needs to be directed toward increasing the recruitment from the less productive stocks in a mixture, rather than obtaining still larger recruitments from stocks that are already doing well.

12. In principle, Mechanism 1 should apply to all species of fish in which the period of increasing rate of exploitation is longer than an average generation of the fish's life. However, for species other than Pacific salmon the balance between growth and mortality needs to be considered in order to determine its effect on the weight of catch obtained.

13. Mechanism 2 can apply to any species in which more-or-less discrete stocks are fished together, or to common fisheries for two or more species characterized by different productivities.

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Relation Between Total Body Weight and Concentrations of Manganese, Iron, Copper, Zinc, and Mercury in White Muscle of Bluefish (*Pomatomus saltatrix*) and a Bathyl-Demersal Fish *Antimora rostrata*

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CROSS, F. A., L. H. HARDY, N. Y. JONES, and R. T. BARBER. 1973. Relation between total body weight and concentrations of manganese, iron, copper, zinc, and mercury in white muscle of bluefish (*Pomatomus saltatrix*) and a bathyl-demersal fish *Antimora rostrata*. J. Fish. Res. Board Can. 30: 1287–1291.

Concentrations of mercury (Hg) increased significantly with size ($P<0.001$) in white muscle of bluefish (*Pomatomus saltatrix*) and a bathyl-demersal fish *Antimora rostrata* but concentrations of manganese (Mn), iron (Fe), copper (Cu), and zinc (Zn) either remained constant or decreased. These results indicate that fish residing in two different ecosystems in the Atlantic Ocean may be in a steady state with their environment with respect to Mn, Fe, Cu, and Zn but not Hg. The observed variations in accumulation patterns of trace metals in muscle of these two species as a function of size are discussed.

CROSS, F. A., L. H. HARDY, N. Y. JONES, AND R. T. BARBER. 1973. Relation between total body weight and concentrations of manganese, iron, copper, zinc, and mercury in white muscle of bluefish (*Pomatomus saltatrix*) and a bathyl-demersal fish *Antimora rostrata*. J. Fish. Res. Board Can. 30: 1287–1291.

La teneur en mercure (Hg) augmente de façon significative en fonction de la taille ($P < 0.001$) dans le muscle blanc du tassergal (*Pomatomus saltatrix*) et de l'antimore bleu (*Antimora rostrata*), un poisson bathydémersal, mais les teneurs en manganèse (Mn), fer (Fe), cuivre (Cu) et zinc (Zn) demeurent constantes ou diminuent. Ces résultats démontrent que des poissons habitant deux écosystèmes différents de l'océan Atlantique peuvent être dans un état d'équilibre avec leur environnement par rapport à Mn, Fe, Cu et Zn mais non Hg. La discussion porte sur les variations observées dans le schéma d'accumulation des traces de métaux chez chez ces deux espèces en fonction de la taille.

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LITTLE is known concerning environmental and physiological processes that regulate the concentrations of trace metals in marine organisms. Recently it has been shown that concentrations of total Hg increased with age in whole body of lake trout (*Salvelinus namaycush*) (Bache et al. 1971) and in muscle of northern pike (*Esox lucius*) (Johnels and Westermark 1969), spiny dogfish (*Squalus acanthius*) (Forrester et al. 1972), three species of tuna, *Thunnus thynnus*, *T. albacora*, and *T. alalunga* (Cumont et al. 1972), and a bathyl-demersal fish *Antimora rostrata* (Barber et al. 1972). In contrast, concentrations of Mn, Fe, and Zn decrease with size in whole juvenile estuarine fish (Cross and Brooks 1973) as do concentrations of Cu and Zn in whole striped bass fingerlings (*Morone saxatilis*) for wet weights less than 15 g (O'Rear 1971). For striped bass ranging from 15 to 60 g, concentrations of Cu and Zn were constant with weight. Concentrations of cadmium (Cd) in whole body of 1-to 12-year-old lake trout were not age dependent (Lovett et al. 1972). Thus, concentrations of Mn, Fe, Cu, Cd, and Zn either decrease or remain constant in whole fish as a function of age (weight, length) but concentrations of Hg increase with age in both muscle and whole fish.

Except for the studies on Cd and Hg in lake trout, concentrations of both transition metals and Hg have not been analyzed in the same samples of different sized fish. In addition, the relation between the bioaccumulation of transition metals and age in muscle tissue of marine fish is unknown. The purpose of this study is to compare the relation

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between total body weight and concentrations of Hg with that of four biologically-essential transition metals (Mn, Fe, Cu, and Zn) in white muscle of two species of marine fish that inhabit different environments in the Atlantic Ocean. These species were bluefish (*Pomatomus saltatrix*), an epipelagic carnivore found in coastal waters of the western Atlantic Ocean, and a bathyl-demersal morid *Antimora rostrata* collected from 2500-m depth.

Methods

COLLECTION PROCEDURES

Bluefish were caught by hook and line in coastal waters of North Carolina near either Morehead City or Cape Hatteras between June 1971 and March 1972. The fish were weighed, measured, and filleted. The fillets, minus skin, scales, and red muscle were frozen until chemical analyses were begun.

Morids were collected from the upper continental rise, southeast of Cape Hatteras (34°18.2′N 75°32.6′W) in July 1972 by trawling. Upon return to the laboratory, the fish were thawed, filleted, and the white muscle subjected to chemical analyses described below.

ANALYTICAL PROCEDURES

Concentrations of total Hg were measured by the method described for our laboratory by Barber et al. (1972) in five replicate 0.5-g samples of axial muscle from the mid-dorsal region of each fish.

Concentrations of Mn, Fe, Cu, and Zn in white muscle were measured in 100-g samples of bluefish and in 50-g samples in the morids by the method described in Cross and Brooks (1973). Because fish of various sizes were used, the 100- or 50-g samples consisted of entire fillets in smaller fish but only the anterior portion of one fillet in the larger fish. This approach would be valid only if concentrations of these metals were distributed evenly throughout the length of the fillets. To verify this point, we filleted and skinned a 1200-g bluefish, obtained three 50-g segments from the anterior, middle, and posterior regions of each fillet and determined concentrations of Mn, Fe, Cu, and Zn in each segment. Results of this test indicate that concentrations of Mn, Fe, and Zn were distributed evenly throughout the samples (Table 1). Concentrations of Cu differed between the two fillets by 0.08 μg/g — a difference deemed not significant for the purposes of this study.

Results and Discussion

The relation between total body weight and concentrations of Hg in white muscle of both species was significantly different from that found for Mn, Fe, Cu, or Zn (Fig. 1). Concentrations of Hg in muscle of both bluefish and morids increased significantly ($P<0.001$) as a function of total body weight while concentrations of Mn, Fe, Cu, and Zn did not. Manganese was not related significantly to body weight in either species as was the case for Fe in morids and Cu and Zn in bluefish. Concentrations of Fe in bluefish and Cu and Zn in the morids decreased significantly as a function of total body weight although r^2 values were very low.

These results indicate that fish residing in two different ecosystems in the Atlantic Ocean may be in steady state with their environment with respect to Mn, Fe, Cu, and Zn but not Hg. The four transition metals are required metabolically by living organisms and these fish may be actively regulating concentrations of essential metals in their tissues. The extremely high electronegativity of Hg relative to the other four metals, the resultant high affinity of both inorganic and methyl compounds of Hg for sulfhydryl groups (Gavis and Ferguson 1972), and the high lipid solubility of methyl Hg could reduce the capacity of fish to regulate concentrations of Hg in their tissues. Although the ratio of methyl Hg to the inorganic compounds of Hg in the ocean is not known, it has been shown to constitute 64–94% of the total Hg in muscle of three species of tuna (Cumont et al. 1972). This high affinity of inorganic and methyl Hg compounds for living organic matter can be illustrated by estimating concentration factors for these metals in muscle of bluefish relative to seawater (Table 2). The estimated concentration factor for Hg is almost twice as large as those for Fe and Zn and more an order of magnitude larger than for Mn and Cu. Because the concentration of Hg in muscle of bluefish is dependent upon body size, the concentration factor will vary from about 1000 in young fish to about 6000 in the largest fish analyzed in this study.

This difference in the accumulation patterns between Hg and the other four metals may be related to the interdependency of uptake and elimination rates of elements. If the elimination

TABLE 1. Concentrations of trace metals (μg/g wet weight) in 50-g segments of white muscle from a 1200-g bluefish.

Segment[a]	Mn	Fe	Cu	Zn
F-1, S-1	0.26	4.8	0.51	4.5
F-1, S-2	0.24	4.8	0.58	5.0
F-1, S-3	0.25	4.9	0.57	4.6
F-2, S-1	0.28	4.6	0.44	5.2
F-2, S-2	0.22	5.0	0.49	4.7
F-2, S-3	0.20	4.5	0.49	4.7

[a] F=fillet number, S=segment number.

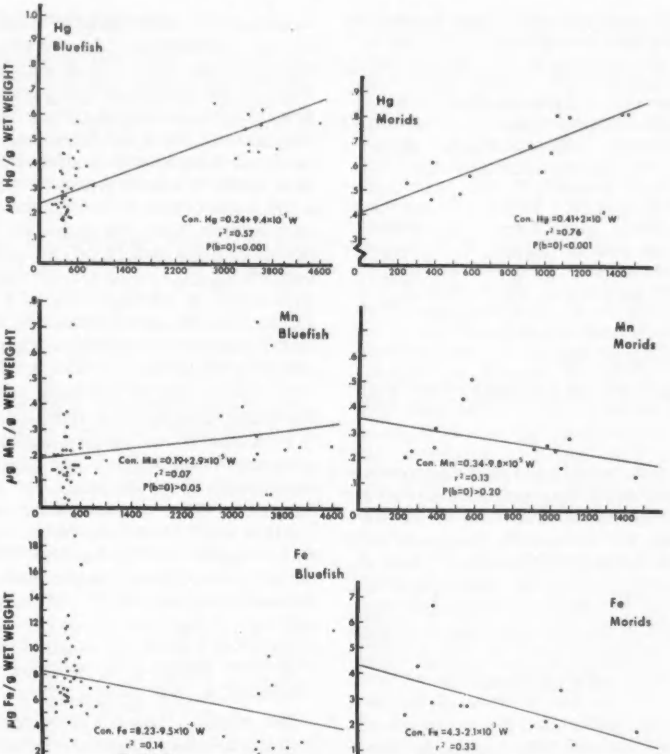

FIG. 1. Relation between total body weight and concentrations of trace metals in white muscle of bluefish and morids. Each point represents analysis of an individual fish and the term "W" in the equations represents the wet weight of the fish.

TABLE 2. Estimated concentration factors for Mn, Fe, Cu, Zn, and Hg in muscle of bluefish.

Element	Seawater concn (μg/liter)	Mean muscle concn (μg/g wet weight)	Concn factor
Mn	2[a]	0.22	110
Fe	3[a]	7.0	2300
Cu	3[a]	0.61	200
Zn	3[b]	6.4	2100
Hg	0.1[b]	0.37	3700

[a] From Goldberg et al. (1971).

[b] From Baseline Studies of Pollutants in the Marine Environment and Research Recommendations (1972).

rate of Hg from fish muscle is not entirely dependent upon the uptake rate, the concentration of Hg in the muscle may be dependent upon the environmental levels of biologically available Hg. Johnels and Westermark (1969) showed that the relation between Hg content of axial muscle and total body weight in pikes was dependent upon the lake from which the fish were collected. Each lake contained different levels of Hg pollution (Wallace et al. 1971) which affected the net accumulation rate of Hg in muscle tissue of the pike. Pike from Lake Snogekolm had the lowest concentration of Hg and showed only a slight net accumulation with age indicating that the environmental level of biologically available Hg was apparently lowest in this lake and the elimination rate of Hg from the muscle was very similar to the uptake rate (Wallace et al. 1971).

Environmental levels of biologically available Hg in the ocean must be such that the rate of incorporation into fish muscle exceeds the rate of elimination. Muscle of marine fish, therefore, may never achieve a steady state with environmental levels of Hg throughout their entire lives. If this hypothesis is true, the life expectancy of the fish would be an important factor in determining the absolute level of Hg attained in their muscle. Because the oldest fish in the ocean are often carnivorous, much attention has focused on the trophic level of the fish rather than their age.

In contrast to Hg, elimination rates of transition or essential metals may be more nearly dependent upon uptake rates. Bryan (1964 and 1967) demonstrated that the lobster, *Homarus vulgarus*, and the shore crab, *Carcinus maenus*, had the capacity to regulate concentrations of Zn in muscle when exposed to unusually high concentrations of Zn in both food and water. In addition, the rate of loss of accumulated ^{65}Zn was increased in starved crabs (Bryan 1967) and amphipods (Cross et al. 1969) by the feeding of nonradioactive food indicating that the elimination rate of ^{65}Zn (and therefore Zn) was increased by increasing the uptake rate of Zn. The maintenance of similar concentrations of a metal in muscle tissue throughout the life of a fish suggests that, except for trace metals accumulated by new tissue, the exchange rates of the metal between muscle and blood are essentially constant over the life-span of the fish. The significant decrease with weight in concentrations of Fe in bluefish and Zn and Cu in morids could be due to compositional changes in muscle, a decreased intake of metals in the diet of older fish, or dilution by growth.

Our interpretation of these data is based upon the assumption that the accumulation pattern for Hg in both bluefish and morids resulted from naturally occurring levels of Hg in the ocean. The relatively insignificant effect that man has had on the mass balance of Hg in the marine environment has been discussed previously (Weiss et al. 1971; Gavis and Ferguson 1972; Baseline Studies of Pollutants in the Marine Environment and Research Recommendations 1972; Hammond 1971). In addition, analyses of Hg concentrations in muscle of preserved marine fish caught 90 years ago (Miller et al. 1972; Barber et al. 1972) are similar to values obtained from fish caught recently.

The results obtained from this study indicate that accumulation patterns of trace metals in fish muscle can vary as a function of the species of fish, its size, and the metal analyzed. If concentrations of a trace metal such as Hg vary in fish muscle as a function of age, then interspecific comparisons for that metal can be made only among fish of the same age. It has yet to be determined, however, if the positive correlation between concentrations of Hg in fish muscle and total body weight is peculiar for only Hg, for metabolically nonessential trace elements, or limited to a small number of elements. We also must determine if metabolic energy is expended by fish to maintain relatively constant concentrations of metals in muscle, as found for Mn, Fe, Cu, and Zn.

Additional studies on other species and metals need to be conducted so that we can describe the baseline levels of trace metals in marine organisms and understand the processes that regulate trace metal concentrations in their tissues. The use of ratios of elements to detect toxic metal contamination as suggested by Patterson (1972) and Hugget et al. (1973) also requires a thorough knowledge of the distributional patterns of trace metals throughout the ecosystem studied.

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Uptake of Methyl Mercuric Chloride and Mercuric Chloride by Trout: A Study of Uptake Pathways into the Whole Animal and Uptake by Erythrocytes in vitro

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OLSON, K. R., H. L. BERGMAN, AND P. O. FROMM. 1973. Uptake of methyl mercuric chloride and mercuric chloride by trout: a study of uptake pathways into the whole animal and uptake by erythrocytes in vitro. J. Fish. Res. Board Can. 30: 1293–1299.

Twenty-four hour uptake rate of either $^{203}\mathrm{HgCl}_2$ or $\mathrm{CH}_3{}^{203}\mathrm{HgCl}$ by rainbow trout (*Salmo gairdneri*) was not affected by esophageal ligation. Uptake of these two mercurials in nonfeeding trout appears to be by way of the gills. Methyl mercury enters the fish at a faster rate than the inorganic form and anomalous tissue distribution of these two mercurials suggests that inorganic mercury does not require methylation prior to entry into the fish.

In vitro experiments using radioactive mercurials demonstrated high affinity of methyl mercury for red cells (up to 90% was bound to red cells in 40 min). Only 9% of inorganic mercury was taken up by red cells, but, this percentage was increased up to 65% if the cells were washed and suspended in Ringer solution prior to incubation with mercury.

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Le taux d'absorption, par 24 h, de $^{203}\mathrm{HgCl}_2$ ou $\mathrm{CH}_3{}^{203}\mathrm{HgCl}$ par la truite arc-en-ciel n'est pas affecté par la ligature de l'oesophage. L'absorption de ces deux composés mercuriels par des truites qui ne mangent pas semble se faire par voie des branchies. Le mercure-méthyle pénètre dans le poisson à un taux plus rapide que la forme organique, et la distribution de ces deux composés mercuriels dans les tissus suggère que le mercure inorganique ne requiert pas de méthylation avant son entrée dans le poisson.

Des essais in vitro avec des composés mercuriels radioactifs démontrent la haute affinité du mercure-méthyle pour les cellules rouges (jusqu'à 90% est lié aux cellules rouges après 40 min). Seulement 9% du mercure inorganique est absorbé par les cellules rouges; cependant, ce pourcentage monte à 65% lorsque les cellules sont lavées et mises en suspension dans une solution de Ringer avant incubation en présence de mercure.

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UPTAKE of mercury by fish can occur via three possible routes, the gastrointestinal (GI) tract, the skin, or the gills. The importance of the GI tract in mercury uptake has been demonstrated by Hannerz (1968), Backström (1969), Miettinen et al. (1969, 1970), Miettinen (1970), and others. Although orally administered mercury was often regurgitated in their experiments, the general consensus was that mercury, especially methyl mercury, is absorbed through the GI pathway. Fecal excretion rates, as low as 8% of the administered dose, accompanied by high tissue levels following force-feeding of methyl mercury or other Hg-organics supported this contention.

In nonfeeding, freshwater teleosts, which also accumulate high tissue levels of mercury, the amount of mercury absorbed via the GI tract may be limited by a low drinking rate (around 13 µliters/hr per 100 g for a freshwater adapted eel (Maetz and Skadhauge 1968)). However, if exposure to mercury stimulates drinking rates, the GI tract pathway could play a significant role in mercury uptake. To our knowledge there have been no efforts to delineate the importance of each of these pathways in nonfeeding teleosts.

Following uptake by the fish, the transport of mercury to the tissues is undoubtedly by way of the circulatory system. Little is known of the relative distribution of mercury between plasma and cellular fractions in nucleated erythrocytes. Rucker and Amend (1969) reported that ethyl mercuric phosphate was found mainly in the cellular fraction of rainbow trout blood with only traces in the serum. However, no quantitative data were presented.

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Backström (1969) found that quail red blood cells (RBCs) had a decreasing affinity for methyl, phenyl, and methoxyethyl mercury, respectively. At 1 hr post-injection the cell/plasma concentration ratios of mercury had decreased from around 32 to 26 to 4.4 for these compounds. For inorganic mercury (Hg^{++}) he reported cell/plasma ratios of around 0.8 (for quail blood) indicating a decreased cellular uptake by quail erythrocytes.

In mammalian blood organic mercurials are primarily associated with the cellular fraction (Swensson et al. 1959a, b; Norseth and Clarkson 1970). There is wide variation in the distribution of inorganic mercurials in the blood of mammals and RBC/plasma ratios ranging from 0.4 to 1.0 have been reported for human blood (Swensson et al. 1959; Lundgren et al. 1967; Rahola et al. 1971; and Miettinen, in press, quoted by Friberg and Vostal 1970). Swensson et al. (1959) report that in rat blood "nearly all of the Hg^{++} appears in plasma," whereas calculations from the data of Potter et al. (1972) indicate that in blood from cows dosed with $HgCl_2$, 86% of the Hg^{++} is found in the red cells.

The purpose of the experiments reported below was to identify the uptake pathway for mercury in nonfeeding trout and to ascertain some of the properties of mercury interaction with teleost-nucleated erythrocytes.

Materials and Methods

Rainbow trout (*Salmo gairdneri*) weighing 50–70 g were obtained from the Great Lakes Fishery Laboratory, Bureau of Sport Fisheries and Wildlife at Ann Arbor, Mich. At East Lansing they were kept in fiberglass tanks that were continuously flushed with water at 13 C.

In order to determine the significance of the GI tract in mercury uptake by nonfeeding trout, the GI pathway was eliminated in one group of fish by esophageal ligation. The fish were divided into three groups: control, sham ligated, and ligated. The purpose of the sham ligation procedure was to determine if any mercury was taken up through the body wall incision.

Prior to surgery the fish were anesthetized with tricainemethane sulfonate (M.S. 222) and placed ventral side up in a trough. Gill ventilation and anesthesia were maintained by a pulsatile flow of aerated M.S. 222-treated water through a rubber tube which was placed in the oral cavity. A 30–40 mm incision was made on the ventral side about 3–4 mm lateral and parallel to the midline. The anterior portion of the incision approached but did not penetrate the pericardial sac. The anterior portion of the stomach was located and ligated with heavy thread after which the incision was closed with 9-mm wound clips. Sham surgery was performed in a similar manner except that the anterior stomach was located but not ligated. All animals were allowed to recover for 6 days before exposure to the mercury solution. Autopsies revealed that most of the stomach ligatures were intact throughout the experiments. If not, the data were excluded from the statistical analyses.

Eight fish from each group (control, sham, and ligated) were placed into 100 liters of aged tap water that contained 275 ng/liter Hg as either $^{203}HgCl_2$ or $CH_3{}^{203}HgCl$. After 24-hr exposure fish were randomly removed and blood samples taken from the caudal vein. They were then killed and tissue samples from the gills, liver, kidney, heart, skeletal muscle, stomach, and intestine were removed and placed into preweighed vials.

Tissue activity was determined with a 2-inch thallium activated sodium iodide [NaI(Tl)] crystal (Nuclear Chicago well detector) and Nuclear Chicago analyzer/scaler. The tissues were then dried at 110 C for 48–72 hr to determine dry weights. Comparison of tissue wet: dry weight ratios was made as a check on the leakiness of the closed incision, i.e. tissue hydration of the operated groups would be a good indication of water and radioactive mercury uptake through an open incision. Analysis of the data was done on a Control Data Corporation (CDC) 6500 computer. One way analysis of variance was used for all statistical comparisons.

The distribution and cellular uptake of mercury in blood was determined by incubation (at 14 C) of either $^{203}HgCl_2$ or $CH_3{}^{203}HgCl$ with the blood sample and subsequent separation of the cell and plasma components by centrifugation.

Heparinized whole blood or washed cells (washed three times in 3 volumes Ringer solution and resuspended in Ringer solution to give a hematocrit approximately the same as the whole blood) were placed in 25-ml stoppered Erlenmeyer flasks. The mercury solution was added to the blood at time zero and the flasks stirred at 16 rpm with a multipurpose rotator. At timed intervals 0.2 ml of blood was removed and placed in a 0.4-ml polyethylene microcentrifuge tube and centrifuged in a Beckman Microfuge. The supernatant was drawn off and placed in a second microcentrifuge tube. Packed red cells were then resuspended in Ringer soultion, centrifuged, and the subsequent supernatant (wash) was placed in a third microcentrifuge tube. Hematocrits were determined in duplicate for all blood samples incubated.

The concentration of mercury from the packed red cells, plasma, and wash was determined by scintillation counting. Percent uptake of mercury into the cellular fraction was standardized by correction for equal volumes of red cells and plasma according to the following formula:

$$\%\ \text{Incorporated into RBC} = \frac{\frac{1 - \text{Hct}}{\text{Hct}} \times \text{C}}{\frac{1 - \text{Hct}}{\text{Hct}} \times \text{C} + \text{P} + \text{W}} \times 100$$

where; Hct = hematocrit

C = activity in red cell fraction
P = activity in plasma fraction
W = activity in wash

All glassware used was coated with silicone (Siliclad®, Clay Adams, Inc., N.Y.) to minimize adsorption of the mercurial onto the glass.

Results and Discussion

Uptake of divalent mercuric ions, as well as methyl mercuric ions, occurs primarily by way of the gills (Table 1). Ligation of the esophagus has no apparent effect on 24-hr accumulation of either form of mercury by any tissue with the exception of gills from fish exposed to inorganic mercury. In this instance gills from the sham-operated fish had the highest mercury concentration. There was a noticeable trend, although not statistically significant, toward increased tissue mercury concentrations for sham-operated fish in both experiments. The explanation for this is unknown but possibly related to variations in surgical trauma.

In both methyl and inorganic mercury-exposed fish, ratios of tissue dry weight to tissue wet weight remained constant for all tissues except liver and kidney. Even though there was an increase in hydration of liver and kidney tissue the change was no greater than 1.5% and probably does not reflect gross inward water flux which would be needed to significantly affect tissue mercury concentrations.

Methyl mercury was taken up by all tissues at a much faster rate over the 24-hr experimental period and the large concentration differences in gill tissue observed between the two compounds can be explained only by faster penetration of the methylated form. Mucus which continually coats the gill epithelium can act as an ion binding resin to trap mercury and prevent its access to the tissue. Since ambient concentrations of both mercurials were identical for the experiments and, assuming both ion species were trapped or precipitated by the mucus, the concentration of inorganic mercury at the gill should be no less than one half of the organic form. This is based on the assumption that one sulfhydryl (SH) binding site is occupied by each CH_3Hg^+ ion and a maximum of two SH sites by each Hg^{++}. A ratio of gill methyl mercury concentration to gill inorganic mercury concentration (see below) of 14.4 indicates that the increased uptake of the methylated form must reflect either entry of mercury into the gill tissue where additional binding sites are available or increased mucus secretion which binds the methylated form on the exterior of the gill. Observations of fish from this and numerous other experiments have shown that methyl mercury is not a greater stimulus to mucus secretion than inorganic mercury and, in fact, the opposite is often the case. The increased penetration of methyl mercury into gill tissue may simply reflect the greater lipid solubility of this compound over that of inorganic mercury. This explanation would hold if mercury gains entry into gill epithelial cells across a lipid-containing cell membrane and not via water-filled pores. On the other hand the bivalency of inorganic mercury may promote tighter binding to mucoproteins thereby restricting its diffusion into gill tissue.

Comparison of the distribution of the two mercury compounds within a tissue demonstrates preferential accumulation of mercury based on its chemical form. Ratios of methyl mercury to inorganic mercury in various tissues after a 24-hr exposure were as follows:

Gill	14.4
Liver	11.3

TABLE 1. Effect of esophageal ligation on 24-hr uptake of 275 ng/liter mercury as either $HgCl_2$ or CH_3HgCl.

	Tissue activity (ng Hg/g dry weight)					
	$HgCl_2$ Control	Sham	Ligated	CH_3HgCl Control	Sham	Ligated
Gill	28.08±1.381[a]	37.31±1.857	30.54±1.331	404.6 ±24.74	580.9 ±47.29	557.8 ±39.3
Liver	2.60±0.387	2.96±0.246	2.72±0.331	29.3 ± 2.794	40.4 ± 4.993	29.9 ± 4.184
Stomach	2.34±1.155	1.75±0.654	0.99±0.160	9.64± 1.055	10.81± 0.988	9.79± 2.112
Intestine	12.26±5.080	2.14±0.786	2.02±0.698	15.92± 2.591	16.77± 2.160	13.88± 3.477
Heart	2.60±0.206	3.42±0.357	3.30±0.916	30.65± 3.139	48.37± 6.737	41.18± 6.548
Kidney	4.64±0.570	5.43±0.447	4.28±0.332	92.07±13.563	118.12±11.316	92.92± 9.567
Muscle	0.16±0.021	0.18±0.039	0.18±0.015	2.39± 0.439	2.34± 0.274	1.96±0 .399
Blood	15.38±1.166	21.63±2.230	17.70±1.626	81.82± 9.073	141.34±13.542	131.05±20.530
No. of observations	8	8	8	8	7	5

[a] One group is significantly different from the other two ($P < 0.05$) one way ANOVA. Mean±SE.

Stomach	3.5
Intestine	1.3
Heart	11.8
Kidney	19.8
Muscle	15.4
Blood	5.3

The magnitude of these ratios is partially attributable to increased uptake of methyl mercury by the gill, however, all the tissues should exhibit approximately the same ratios if there is no selectivity by the tissues for specific forms of mercury. The differences in these ratios show that tissues such as the kidney, muscle, gill, heart, and liver preferentially accumulate the methylated form and blood, stomach and intestine do not. Low ratios for the latter three tissues could be due to selective accumulation of the inorganic form which is masked by higher uptake rates of the organic compound. Using radio-autography Halbhuber et al. (1970) have demonstrated selective accumulation of $^{203}Hg^{++}$ by the Paneth cells in the intestine of the rat and guinea pig. It was postulated that one function of these cells is to transfer divalent heavy metal ions from the body fluids into the lumen of the gut. Similarly Paneth cells in the trout gut might sequester divalent mercury but not methylated forms.

Uptake ratios of phenylmercuric acetate: mercuric acetate calculated using the data of Ellis and Fang (1967) also show a preferential increased tissue accumulation of the organic mercurial 24 hr after oral administration to rats. Calculated ratios were highest for blood (44) followed by liver (10), heart (6), kidney (2.5), and muscle (1.7). These ratios vary considerably from those calculated for trout and may reflect differences between methyl and phenyl mercury with respect to tissue binding or to the pathway for uptake, i.e. intestinal versus branchial routes.

Backström (1969) administered methyl and inorganic mercury intravenously to speckled trout. After 24 hr the distribution patterns of methyl mercury were similar to our data for rainbow trout with the exception of the low values for the gills. He reported highest inorganic mercury concentrations in the kidney; values for blood and gill were approximately 50% lower. These small discrepancies in distribution, when compared to data presented in this paper are probably due to the mode of administration of the mercurial. The tissue mercury distributions reported by Hannerz (1968) for cod exposed for 24 hr to waterborne mercurials are similar to those found in the present study. He postulated gill uptake as the principal mode of entry of mercury into cod and pike.

In a brief summary of the literature Jernelöv and Lann (1971) have stated that inorganic mercury can be methylated outside the fish possibly by micro-organisms contained in the mucus, or enter as inorganic mercury via the skin, gill, or GI tract. The wide variation in organic/inorganic tissue concentration ratios that we found supports the idea that inorganic mercury can cross the gill epithelium as Hg^{++} or some complex without prior methylation.

The present experiments have eliminated the GI tract as a major pathway for mercury uptake in nonfeeding trout. Most probably, uptake of mercury through the skin is minimal. Bentley (1962) has described the relative impermeable nature of the teleost skin and Evans (1969) and Motais et al. (1969) have shown that, compared to the gill, the skin plays a minor role in diffusional water fluxes. In addition, Knoll (1962) reported the inability of hexavalent chromium to penetrate the skin of rainbow trout. The previously demonstrated permeability of the gill to mercurials (Hibiya and Oguri 1961) and relative impermeability of the skin, coupled with data of the present experiment, support the assumption that the gill is the primary uptake pathway for mercury in nonfeeding trout.

UPTAKE RATES AND PERCENT INCORPORATION OF MERCURY INTO RED CELLS:

The percent uptake of both mercurials into erythrocytes as a function of time is plotted in Fig. 1. With the exception of methyl mercury incubated with whole blood, equilibrium was reached in less than 10 min. Uptake of methyl mercury did not reach equilibrium when incubated with whole blood until after 30–40 min. Analysis of this reaction revealed a two-component uptake system, the first having a half time of under 1 min, the second about 11 min. (Uptake values of less than 1 min are only estimates due to the inherent time lag incurred during blood centrifugation and separation.) This can be explained by initial binding of a small percentage of mercury to plasma proteins or thiols, the remainder being taken up by the red cells as a function of the free or nonplasma bound mercury. After the red cells have removed most of the unbound mercury from the plasma a new equilibrium (slow component) is established that is dependent on the dissociation of bound mercury from "plasma sites" prior to red cell uptake. This postulate is further supported by the mode of uptake of methyl mercury into red blood cells suspended in Ringer solution. In this instance the uptake rate is so fast that only one component can be determined. The increased CH_3Hg^+ binding at equilibrium by washed cells in Ringer solution compared to cells in plasma (95% vs. 90%) is probably indicative of some irreversible mercury binding to plasma protein.

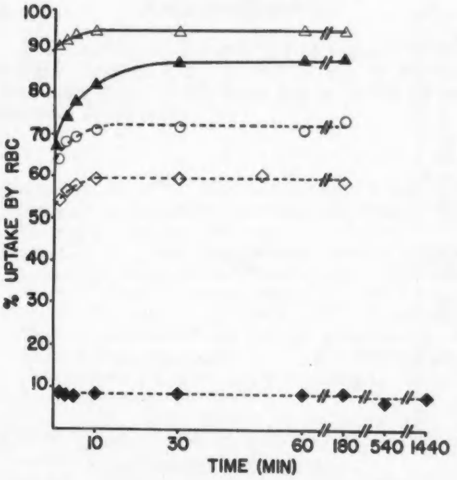

FIG. 1. Percent uptake of methyl mercury or divalent mercury by red blood cells as a function of time. ▲ = CH_3HgCl incubated in whole blood (15); ◆ = $HgCl_2$ in whole blood (6); △ = CH_3HgCl incubated with washed cells suspended in Abbott Ringer (4); ◊ = $HgCl_2$ incubated with washed cells suspended in Abbott Ringer (4); ○ = $HgCl_2$ incubated with washed cells suspended in Phosphate Buffered Ringer (4). Exposure concentrations approximately 0.0133 total ppm CH_3HgCl and 0.054 ppm total $HgCl_2$. Number of observations (N). Standard errors are not shown on the graph as they were smaller than the diameter of the data points.

Failure of the washed cells to bind 100% of the mercury could be due to slight hemolysis coupled with some mercury binding by the incubating media or adsorption on glassware.

Inorganic mercury incubated with whole blood binds almost exclusively to the plasma fraction; less than 9% was taken up by red cells after 1440 min. Such a distribution could explain why in vivo, methyl mercury produced ultrastructural abnormalities in erythrocytes and inorganic mercury did not (Olson and Fromm 1973).

Washed red cells suspended in Ringer solution take up 9–10 times more inorganic mercury than cells do in plasma. Removal of plasma proteins undoubtedly is the critical factor. There is also a significant difference in percent uptake by red cells that is dependent on the suspending media; cells suspended in Abbott Ringer take up less Hg^{++} than cells suspended in phosphate buffered Ringer (PBR) solution. Since the only difference between Abbott Ringer and PBR is the presence of magnesium and the buffering capacity of the PBR, either the magnesium or *p*H (perhaps both) must enhance equilibrium binding by red cells. Weed et al. (1962) compared the effects of buffered to unbuffered solutions of saline on Hg^{++} uptake by human red cells and found no effect even if the *p*H of the unbuffered solution was decreased to 6.8. Thus magnesium or some other unaccounted for parameter must be the important factor(s).

Less than 100% of the available methyl or inorganic mercury was taken up by red cells. LeFevre (1947) found that the effect of mercury on the uptake of sugar by mammalian red cells was reduced if the cells were allowed to stand for some time before addition of mercury. He postulated that there was secretion of a mercury chelator by the cells which after a period of time reached sufficient levels to bind enough mercury to effectively reduce the free mercury available for cellular uptake. Weed et al. (1962) found similar results with respect to inorganic mercury uptake, i.e. the longer the cells were incubated without mercury, the less mercury would be taken up by them after this ion was added. In the present experiments percent mercury uptake before and at equilibrium was calculated for cells to which mercury was added within 1 min after final suspension or whole blood sampling and for cells that had been allowed to stand in Ringer solution or whole blood for 45 min prior to addition of mercury. Uptake of either methyl or inorganic mercury was, in all instances, independent of the length of the incubation period which preceded addition of mercury to the cell suspension. Thus, secretion of a chelator by trout red cells is not a factor in the failure of these cells (especially washed cells) to bind all mercury present.

In an attempt to determine the total number of binding sites in the red cell, washed cells were incubated for 90 min with increasing concentrations of mercury. Weed et al. (1962) have shown that the percent of inorganic mercury bound to the red cell decreases as ambient mercury increases, which is indicative of saturation of specific binding sites on or within the red cell. Figure 2 (open circles) shows the results of his experiment in which increased levels of ambient mercury produced a characteristic saturation curve and the percent mercury bound to the cells decreased from 97 to 39%. These data do not correlate with methyl (open triangles) or inorganic (solid triangles) mercury binding from the present study as the percent mercury bound remained constant for all levels of ambient mercury examined. Ambient mercury levels higher than those plotted produced red cell hemolysis in the trout blood experiments; Weed reported essentially no hemolysis for human erythrocytes at any of the ambient mercury levels employed.

It appears that saturation of trout erythrocytes with mercurials must involve either (1) some group(s) such as SH, amino, or other which are responsible for cell membrane integrity and are not saturated at the time of hemolysis or (2) a disruption of ionic balance and subsequent osmotic hemolysis caused by mercury levels below those required for total cell saturation.

Consistent RBC unbound/bound ratios for either mercurial at all ambient mercury concentrations studied is explainable in terms of a specific binding site theory since at low mercury concentrations a greater percentage of the available mercury should bind to the cell. Why 5% of the methyl mercury and approximately 25% of the inorganic mercury fail to bind to red cells irrespective of a 100,000-fold increase in ambient methyl mercury or a 3,000-fold increase in ambient inorganic mercury concentration is unknown.

Sulfhydryl-containing compounds such as albumin, cysteine, and reduced glutathione failed to remove either inorganic or organic mercury previously bound to red cells (Table 2). In both experiments levels of SH-groups exceeded mercury concentrations at the low ambient mercury levels, yet all SH contributors failed to remove any mercury from the cells, which suggests strong mercury–red cell binding.

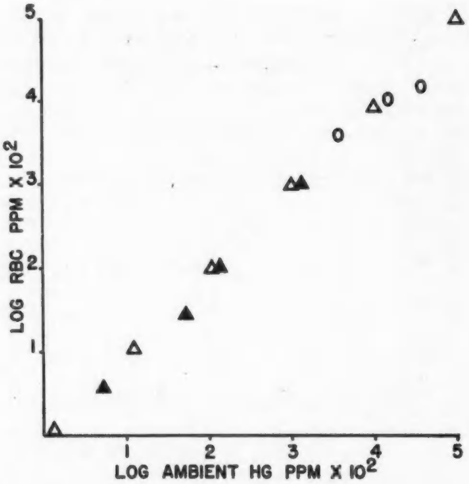

FIG. 2. Concentration of mercury in the red blood cell fraction as a function of ambient mercury levels. ▲ = inorganic mercury, washed trout erythrocytes (4); △ = organic mercury, washed trout erythrocytes (4); ○ = data from Weed et al. (1962), washed human erythrocytes (2). Number of observations (N). Standard errors are smaller than diameter of data points.

TABLE 2. Effects of sulfhydryl agents on mercury binding to red cells.

	Inorganic mercury					Methyl mercury	
Hg concn ppm total	0.054	0.54	1.454	14.054	140.054	0.1326	1000.0
ppm (mg Hg/liter red cells)	0.387	3.87	10.39	100.39	1000.4	0.947	7143.8
Control % Incorporation into RBC±SE	66.99±3.17[a]	57.06±1.35	74.99±1.94	77.31±0.78	hemolysis	95.15±0.21	96.88±0.68
Effect of SH-groups							
% Incorporation + Albumin (1.37 × 10^{-5}M)	66.85±3.76	59.59±2.22	79.88±1.73	77.38±1.23	–	95.98±0.10	97.44±0.21
% Incorporation + Cysteine (1.37 × 10^{-4}M)	68.78±2.60	64.09±1.78	81.67±1.76	77.97±1.36	–	96.63±0.19	96.63±0.22
% Incorporation + Reduced GHS[b] (1.37 × 10^{-4}M)	61.30±3.07	47.32±2.42	78.66±1.61	74.56±2.58	–	95.84±0.19	96.19±0.11
No. of observations	6	4	6	6		4	4

[a] Mean ± SE
[b] GHS = glutathione.

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Metabolism and Biliary Excretion of Sulfobromophthalein by Rainbow Trout (*Salmo gairdneri*)

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SCHMIDT, D. C., AND L. J. WEBER. 1973. Metabolism and biliary excretion of sulfobromophthalein by rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 30: 1301–1308.

The plasma half-life of sulfobromophthalein (BSP) for rainbow trout (*Salmo gairdneri*) was 13 min for doses of 5 and 10 mg/kg and 29 min for a dose of 15 mg/kg. The biliary BSP transport maximum (Tm) averaged 9.6 μg/min per kg for five fish while the blood clearance averaged 1.7 ml/min per kg for two fish. Normal bile flows of 0.87 μliter/min per kg in trout were increased upon anesthetization but were unaffected in fish allowed to recover from spinal transection. Spinal transection did not affect the plasma half-life of BSP.

The data presented support the conclusion that the transport of BSP from liver cells to bile is the rate-limiting step in the excretion of this dye. When the BSP Tm of trout was compared to literature values for mammals and dogfish (*Squalus acanthias*), large differences were found which were probably caused by effects of different temperatures and blood flows. When the Tm values of the various species were based on blood clearance of BSP (reflecting liver blood flow) the differences were greatly reduced, suggesting similar abilities of the liver of the various species to excrete this dye.

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La demie-vie du sulfobromophthaléine (BSP) dans le plasma de la truite arc-en-ciel (*Salmo gairdneri*) est de 13 min pour des dosages de 5 et 10 mg/kg et 29 min pour un dosage de 15 mg/kg. Le maximum de transport (Tm) du BSP biliaire a une valeur moyenne de 9.6 μg/min/kg pour cinq poissons, alors que le flot sanguin a une valeur moyenne de 1.7 ml/min/kg pour deux poissons. L'écoulement biliaire normal de 0.87 μlitre/min/kg chez la truite augmente avec l'anesthésie, mais ne change pas chez des poissons qui ont pu se rétablir d'une dissection transversale de la colonne vertébrale. Cette dissection n'affecte pas la demie-vie plasmatique du BSP.

Ces données corroborent le point de vue que le transport du BSP des cellules hépatiques vers la bile est l'étape limitante de la vitesse d'excrétion du colorant. Les grandes différences de Tm du BSP entre ces valeurs et celles mentionnées par divers auteurs pour les mammifères et l'aiguillat commun (*Squalus acanthias*) sont probablement le résultat de différences de températures et de flot sanguin. Lorsque le Tm des diverses espèces est basé sur le flot sanguin du BSP, comme mesure du flot sanguin du foie, les différences sont beaucoup moindres, ce qui suggère que le foie des diverses espèces peut excréter ce colorant au même degré.

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INTEREST in the metabolism and excretion of foreign compounds by fish has increased in recent years. Brodie and Maickel (1962) hypothesized that fish lack most liver microsomal enzyme systems because their gills act as an excretory system for the more lipid soluble compounds. Contrary to this hypothesis, Dixon et al. (1967), Adamson (1967), Buhler and Rasmussen (1968), Dewaide (1971), and Lech (1973) found that many of the mammalian drug metabolizing enzyme systems are indeed present in fish. Further, Maren et al. (1968) and Walker (1972) emphasized the relative unimportance of the gills of the dogfish (*Squalus acanthias*) in the excretion of many substances.

Dogfish bile–plasma ratios of several compounds reported by Adamson and Guarino (1972) indicate qualitative similarities between this species and mammals. In a comparative study of organic anion binding proteins from the liver and other tissues, the plasma half-life of the dye, sulfobromophthalein

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(BSP), in the Atlantic mackerel (*Scomber scombrus*) and the dogfish was reported to be substantially longer than the half-life of the same dye in mammals (Levine et al. 1971). Burger (1967), in an analysis of hepatic disposition of BSP in the dogfish, reported values for the rate of plasma decay, transport maximum (Tm), and biliary clearance of BSP that are substantially below those in the literature for mammals. He also calculated hepatic blood flow using BSP. Also using the dogfish, Boyer (1971) compared the excretion rate of BSP with a related dye, phenoldibromophthalein (DBSP). As in mammals, the two dyes are metabolized differently but are excreted at similar rates.

The purpose of this study was to evaluate biliary excretion of BSP in rainbow trout (*Salmo gairdneri*). We chose this dye because it has been extensively studied in mammals and some information on its excretion by dogfish is available. Since this dye was excreted exclusively in the bile of the vertebrates previously studied, its disposition by trout should reflect the comparative excretory capabilities of the trout liver. To obtain a proper perspective of our results, we compared our values with those recorded in the literature for dogfish and mammals.

Materials and Methods

Artificially propagated rainbow trout weighing between 50 and 400 g were used in these experiments. Food was withheld and water temperature was maintained at 12 ± 1 C for at least 4 days prior to experimentation.

Immobilization of the fish was necessary to conveniently collect bile. Spinal transection and anesthetization with M.S. 222 (tricaine methanesulfonate) were two methods which we used and compared in free-swimming fish. Fish were transected by crushing the neural arch and spinal cord approximately 2 cm posterior to the end of the opercula. Bile collection was accomplished by catheterizing the common bile duct with PE 10 tubing and ligating the cystic duct. To obtain a consistent flow of bile, the catheter must be inserted into the bile duct so the open end does not obstruct the hepatic ducts. Much experience with this procedure was necessary to establish the proper distance to insert the cannula. Ligating the cystic duct can be difficult because it is usually imbedded in hepatic tissue. However, this duct could be ligated where it expands into the gall bladder sufficiently close to the junction of the hepatic and bile ducts so that very little of the gall bladder tissue is available for reabsorption of bile fluids. The effects of the remaining cystic duct and gall bladder tissue on bile flow were probably insignificant. Burger (1967) noted high variability in bile flow from dogfish when the cannula was introduced through the gall bladder. We feel that our procedure eliminates much of this variability. All of the bile flow measurements for each fish are the mean of a 5-hr collection period.

In transected fish, bile was collected by placing a surgically prepared fish in a plexiglass chamber fitted with a restraining latex diaphragm. The fish were held by the diaphragm which was stretched around the trunk anterior to the dorsal fin. The bile catheter exited through the bottom of the chamber. Bile was collected in sealable microcentrifuge tubes and quantified by weighing. The specific gravity of the bile was considered to be 1.0 for conversion to units of volume.

To obtain a "normal" bile flow in free-swimming fish for comparison with immobilized fish, a different bile collection technique was used. After cannulation of the bile duct and ligating the cystic duct with PE 10 tubing, the fish were allowed to recover for 24 hr. A piece of volume calibrated PE 190 tubing approximately 20 cm in length was attached to the PE 10 tubing by inserting a polyethylene collar into an open end of the PE 190 tube. This collar fit tightly around the PE 10 bile duct catheter. Bile flow was measured by observing the movement of bile into the calibrated PE 190 tube. This method of bile collection had limitations because movements of the fish caused the catheters to dislodge. Restricting vertical movements of the fish by keeping the depth of the water in the aquarium approximately 10 cm helped alleviate this problem. Bile flow was measured similarly in anesthetized fish. M.S. 222 was added to the water until there was no response to fin pinching but opercular movements remained strong.

Plasma decay of BSP was determined in free-swimming and unrestrained transected fish held in an aquarium. Doses of 5, 10, and 15 mg/kg of BSP in Cortland's saline were injected into the caudal vein. A single blood sample was obtained from each fish by cardiac puncture. Drawing multiple blood samples from a single fish was abandoned because this procedure produced variable results and a general increase in BSP retention.

BSP and metabolite concentrations in the bile were measured, after appropriate dilutions, on a Klett-Summerson colorimeter with a number 54 filter. Blank values were obtained for each sample. The samples were alkalinized with a drop of 10% NaOH before total optical densities of BSP and metabolites in the bile were measured. Molar extinction coefficients of these metabolites were considered to equal the coefficient of BSP for calculations of total quantities of BSP and metabolites; however, this may not be strictly correct since some changes in these coefficients occur in BSP metabolites from mammals (Krebs 1958). Serum concentrations of BSP were determined by the method of Natelson (1961), measuring optical density on a Beckman DB Spectrophotometer. Blank values revealed that the amount of hemolysis occurring in control blood samples did not alter results more than ± 5% of reported values.

The transport maximum (Tm) of BSP and metabolites into bile was determined directly by infusing the dye into a cannulated ventral intestinal vein and collecting bile from the cannulated bile duct. Cannulation of the bile duct, ligation of the cystic duct, and insertion of the intestinal vein catheter were performed immediately before each experiment on unanesthetized fish that had been transected 24 hr previously. The infusion procedure necessitated using only restrained transected fish in these experiments. Heparin (100 U.S.P. units/ml) and sodium citrate (8% solution) were both used as anticoagulants; however, citrate proved to be superior. BSP was infused at a rate near the expected Tm value until the biliary BSP excretion rate stabilized. Infusion for 6 hr at this rate was necessary to obtain a relatively constant BSP excretion rate. After this "steady state" was obtained, the infusion rate was increased 21 μg/min/kg, well above the Tm and continued until biliary BSP excretion no longer increased. This procedure was used to avoid possible toxic effects of high plasma concentrations of BSP. Finally, to insure the Tm had been reached, a 5–10-mg/kg dose was administered following the infusions and biliary BSP excretion was determined for 6–12 hr. The maximum rate of appearance of biliary BSP was considered to be the Tm.

Blood clearance of BSP was determined for two of the fish for which the Tm had been determined. These fish were infused at a rate below the Tm for at least 8 hr. After this period of infusion, the average rate of biliary BSP excretion from two consecutive bile samples was determined. A single blood sample was taken and the hematocrit determined in order to calculate blood clearance by the liver. Clearance values were calculated based on both body and liver wet weight. In addition, the liver and body weights were determined for 38 fish ranging from 150 to 320 g, and liver weight as a percentage of body weight was calculated.

Metabolites of BSP in the bile of fish and rats were compared by simultaneous separation on thin layer chromatograms. Bile was obtained from Sprague-Dawley rats anesthetized with pentobarbital (50 mg/kg). Rats with cannulated bile ducts were given 50 mg/kg BSP intravenously, approximately 10 min before the bile was collected. Beckman cellulose-powder thin layer strips, with appropriate solvent and detection systems (Whelan and Plaa 1963), were used with improved results over previous experiments (Schmidt and Weber 1972).

Excretion of BSP across the gills and into the urine was also tested in fish held in plexiglass chambers. Urine was collected over a 12-hr period from two fish given approximately 15 mg/kg BSP. Collection of urine was accomplished by means of a PE 50 catheter inserted into the posterior portion of the mesonephric duct (bladder). Approximately 1 liter of aerated water that recirculated for 12 hr over the gills of two different fish was analyzed for BSP.

Results

BILE FLOW

Free-swimming, transected, and anesthetized fish were compared to determine the effects of immobilization procedures on bile flow. Transection had no affect on bile flow while anesthetization with M.S. 222 caused a twofold increase (Table 1). Flow rates derived from the literature for dogfish and laboratory rats and mice are included in this table for comparison.

TABLE 1. Effects of immobilization procedures on bile flow of rainbow trout (*Salmo gairdneri*). Values for dogfish (*Squalus acanthias*) and laboratory rats and mice are included for comparison.

Species and condition	No.	Bile flow (*μliters/min/kg*)
Trout–free-swimming	12	0.87 ± .20[a]
Trout–anesthetized	8	2.02 ± .13
Trout–transected	11	0.87 ± .10
Dogfish[b]	–	1.3
Rat[c]	–	64
Mouse[d]	–	25–46

[a] Standard error.

[b] From Burger (1967).

[c] From Klaassen and Plaa (1967).

[d] Calculated from Goldfarb et al. (1962); range of values given.

PLASMA HALF-LIFE

Doses of 5, 10, and 15 mg/kg BSP were used to determine its plasma half-life in trout. The plasma half-life was approximately 13 min when the BSP doses were 5 and 10 mg/kg (Fig. 1.) However, with a 15-mg/kg dose, the half-life increased to 29 min. Blood samples from fish administered 15 mg/kg exhibited considerable hemolysis. In free-swimming fish, a loss of righting reflex and death occurred at higher doses.

BILIARY TRANSPORT MAXIMUM (TM) AND CLEARANCE

Mean biliary excretion values of BSP and metabolites for five fish were plotted against time (Fig. 2). Also plotted were the mean bile flow and the mean biliary BSP concentration. The peak level of biliary BSP excretion was considered to be the Tm. When biliary BSP excretion stabilized, the Tm values obtained from the five fish ranged from 7.3 to 11.8 μg BSP/min per kg of body weight. Futher, the range of concentration of BSP in the bile was from 4.0 to 10.7 mg/ml of bile, while bile flow ranged from 0.68 to 2.98 μliters/min per kg of body weight. When biliary BSP excretion was maximal, variations in bile flow among individual fish were inversely correlated with biliary BSP concentrations. The decrease in bile flow during the experiment, as shown in Fig. 2, may be caused by surgery and handling. This would mask any effect of infusion of BSP on bile flow. Apparently, increases in biliary excretion of BSP were affected by changes in bile concentration of BSP and not by increases in bile flow.

The transport maxima, bile flows, and biliary BSP concentrations of dogfish and mammals are compared with those of trout in Table 2. Differences in the Tm among species parallels differences in the rate of bile formation. Bile flow and Tm values for the trout were also calculated per 100 g of wet liver weight. The Tm was 95 μg/min per 100 g liver, with bile flow averaging 19 μliters/min per 100 g liver. The liver weights of 38 fish ranged from 0.6% to 1.3% body weight, with a mean value of 0.84%. Blood clearance of BSP was calculated for two fish for which the Tm had been determined. Clearance values of 17 and 19 ml blood/min per 100 g of liver or 1.5 and 1.9 ml/min per kg of body weight were determined. Ratios of appearance of BSP and colored metabolites in bile to the infusion rate were 1.36 and 1.64 for each of the two fish after an assumed steady state was obtained. This difference also occurs in mammals and is primarily influenced by a loss in peak extinction coefficients of the metabolized forms appearing in the bile (Krebs 1958).

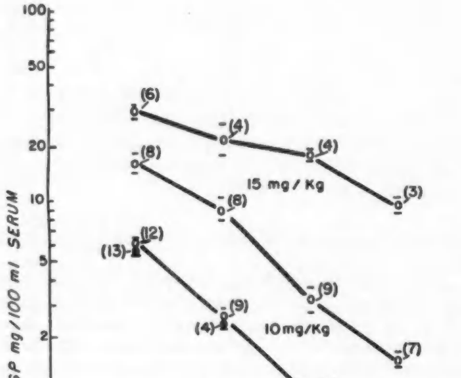

FIG. 1. Plasma decay curve of three different injected doses of BSP in free-swimming rainbow trout (*Salmo gairdneri*). Mean values for plasma concentration of transected fish are included for the smallest dose. Points are the mean values of the number of fish in ().

METABOLISM

Thin layer chromatographic analysis of bile collected from trout and rats revealed no qualitative differences in the metabolism of the dye (Table 3). The apparent difference in at least one metabolic product reported previously (Schmidt and Weber 1972) was caused by the effects of other substances in the bile on the mobility of the fractions during separation. Because Rf values for spots varied considerably between thin layer strips, the mobilities of each fraction separated were compared to the predominant fraction of the rat. Since other substances in the bile had an effect on the migration of fractions, an equal volume of control bile from the other species was mixed with bile containing BSP before spotting on the thin layer strip. Trout and rat control bile was also mixed with the standard BSP. If this procedure was not followed, comparison of similar fractions was impossible. For both species, the three spots with mobilities different from the BSP standard were ninhydrin positive, probably indicating association with amino acids. The metabolites were not quantified, but are ranked in Table 3 in order of magnitude of the density of the respective thin layer fraction. The spots obtained appear to correlate with those in zone I, III, IV, and V obtained by a similar separation system for bile from several mammals by Whelan and Plaa (1963), but the spots in zone II, reported by these authors, were not observed by us in separated bile from either the trout or rat. Boyer (1971) reported three fractions different from BSP, but ninhydrin negative, when this system of separation was used with dogfish bile containing excreted BSP.

EXCRETION BY THE GILLS AND KIDNEY

We attempted to measure elimination of BSP across the gills and excretions into urine. In the two fish studied, no excreted BSP color could be detected by either route after an approximate 15-mg/kg dose of BSP. Elimination by these routes would need to be less than 1% of the dose administered to elude detection.

Discussion

The effects of anesthetization by M.S. 222 on renal function and cardioventilatory parameters of fish have been reported by several authors (Houston et al. 1971; Hunn and Willford 1972). This anesthetic apparently depresses heart rate and blood pressure while causing a transient diuresis, in addition to many other effects. The increase in bile flow we observed with M.S. 222 appears highly significant

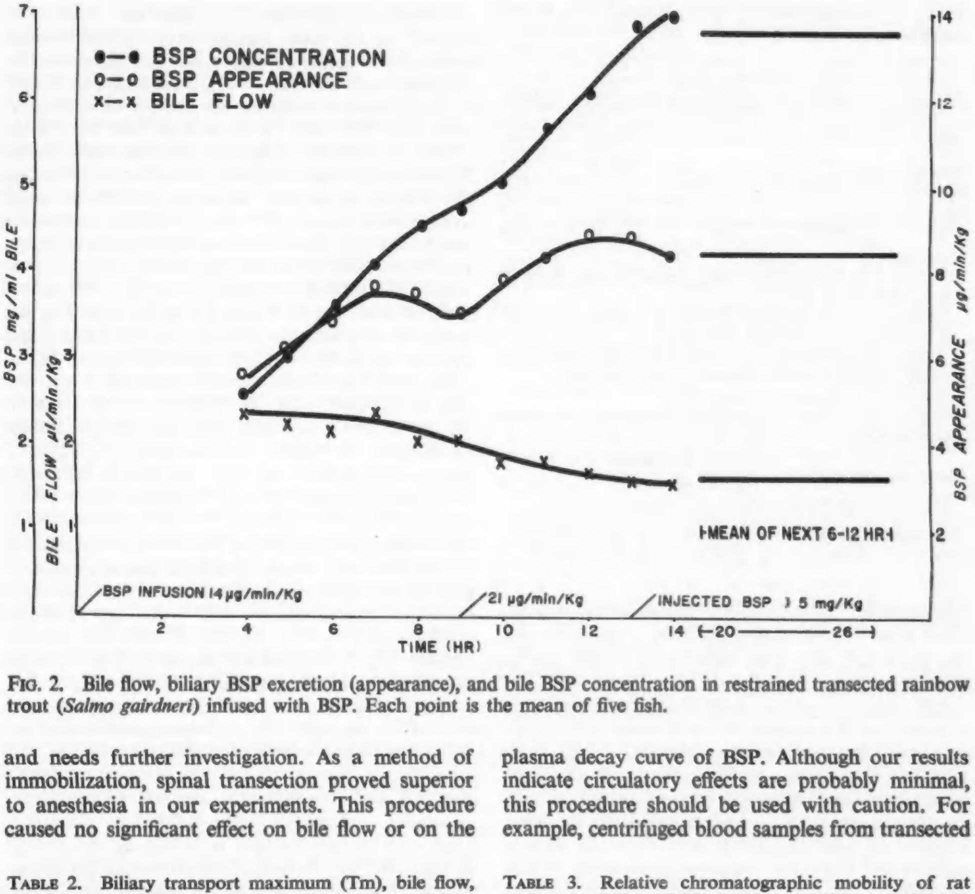

FIG. 2. Bile flow, biliary BSP excretion (appearance), and bile BSP concentration in restrained transected rainbow trout (*Salmo gairdneri*) infused with BSP. Each point is the mean of five fish.

and needs further investigation. As a method of immobilization, spinal transection proved superior to anesthesia in our experiments. This procedure caused no significant effect on bile flow or on the plasma decay curve of BSP. Although our results indicate circulatory effects are probably minimal, this procedure should be used with caution. For example, centrifuged blood samples from transected

TABLE 2. Biliary transport maximum (Tm), bile flow, and maximum biliary BSP concentration for rainbow trout infused with BSP. Literature values for dogfish and three species of mammals used in similar experiments are included for comparison.

Species	Tm (*µg/min/kg*)	Bile flow (*µliters/min/kg*)	Bile BSP (*mg/ml*)
Trout[a]	9.6	1.6	7
Dogfish[b]	23	1.9	12
Rat[c]	950	64	15.6
Rabbit[c]	1130	59	15.7
Dog[c]	170	16	10.6

[a] Mean values of five fish.
[b] Calculated from Burger (1967).
[c] From Klaassen and Plaa (1967).

TABLE 3. Relative chromatographic mobility of rat and trout biliary BSP fractions visible in NH$_4$OH.

Bile source[d]	Relative mobility of similar fractions[a] 1	2	3	4
Rat	1.00[b](1)[c]	1.15[b](2)	1.30[b](4)	1.55(3)
Trout	.97[b](1)	1.11[b](3)	1.28[b](4)	1.52(2)
Control BSP	–	–	–	1.58

[a] Mobility measured relative to rat 1; each value is mean of 3 chromatograms. Fraction numbers were arbitrarily designated; fraction 1 is closest to origin; fraction 4 is closest to solvent front.
[b] Fractions positive to ninhydrin.
[c] Order of density of fractions visualized in NH$_4$OH.
[d] See text concerning preparation of bile before spotting.

TABLE 4. Comparison of BSP Tm/blood clearance ratios among different species.

Species	Tm (*μg/min/kg*)	Clearance (*ml/min/kg*)	Tm/clearance[a]	Index[b]
Trout	9.6	1.7	5.64	1.0
Dogfish	23[c]	.78[c]	29.1	5.2
Rabbit	1042[d]	32.4[d]	32.2	5.7
Dog	170[e]	14.8[f]	11.5	2.0
Man	8400[g]	750[h]	11.2	2.0

[a] Units are micrograms BSP excreted per milliliter blood cleared of BSP.

[b] Ratio of Tm/clearance values of species to trout.

[c] Calculated from Burger (1967).

[d] From Lewis (1950). Blood clearance calculated from plasma clearance using hematocrit equal to 50%.

[e] From Klaassen and Plaa (1967).

[f] Calculated from Casselman and Rappaport (1954) using formula:

$$\text{Blood clearance BSP} = \frac{\text{Hepatic extraction}}{\text{Hepatic blood flow}}$$

[g] In micrograms per minute; from Bradley (1959).

[h] In micrograms per minute; from Popper and Schaffner (1957). Calculated using the formula in footnote f.

fish indicated the hematocrit decreased significantly from that of free-swimming fish. Transection of the spine has also been reported to effect osmoregulation (Lagler et al. 1962).

Although the plasma half-life of BSP has been reported for two species of fish (Levine et al. 1971), care must be used in interpretation of this data. The half-life values of BSP (10-mg/kg dose) of 44 min for the dogfish (*S. acanthias*) and 36 min for the mackerel (*S. scombrus*) reported by these authors are considerably greater than the 13-min half-life we found for rainbow trout using 5- and 10-mg/kg doses. Fig. 1 indicates that even a fourfold decrease in dose (15 mg/kg) from that commonly given small mammals (60 mg/kg) may not be sufficient to give a true picture of the plasma decay. The increase in plasma half-life of BSP that we observed may possibly result from saturation of the transport system and/or the toxity of high plasma concentrations of the dye, since some hemolysis was noted in blood samples at high dose levels. Also, the plasma decay curves of BSP may not be strictly first order as is the case with many mammals (Krebs 1958). In salmonid fish, the length of time necessary for adequate plasma mixing may contribute to the departure from a single first order decay curve (Smith 1966). The possible effects of dose and inadequate plasma mixing on half-life may have affected the values reported by Levine et al. (1971).

Transport maximum has generally been considered as the rate limiting step in the overall process of transfer of BSP from the blood to bile (Whelan and Combes 1971). Metabolism of BSP to conjugates is qualitatively similar in trout and rats, and bile flow rates parallel the Tm values in various species of fishes and mammals (Table 2 and 3). Because of this information, we assume the limitations on the excretion of BSP by trout are also reflected by the Tm. A similar conclusion was reached by Boyer (1971) in dogfish after studying biliary excretion of single doses of BSP and a related compound (DBSP). Although the low Tm values for fish recorded in Table 2 suggest that fish are generally less able to remove this dye from their plasma, temperature effects and the overall metabolic state of the animals are ignored when the Tm is compared on the basis of body weights. To get a more accurate depiction of the ability of different species to excrete this dye, Tm's of the various species were compared on the basis of a physiological rate. We decided that blood clearance of BSP reflects the physiological state of the liver and provides a good basis for comparison of liver function (Table 4). Blood clearance should generally parallel the blood flow through the liver since the extraction of BSP from one passage through the liver is similar in at least the dogfish and the dog. Extraction values are 39.8% for dogs (Casselman and Rappaport 1954) and 32.9% for a single dogfish (Burger 1967), while extraction in humans is near 50% (Popper and Schaffner 1957). Because relatively small fish were used in our experiments, hepatic vein blood samples were not obtained and, consequently, extractions were not calculated. Values in Table 4 for Tm clearance ratios can be considered a reflection of the ability of the liver to eliminate BSP removed from the plasma. The values quoted for dogfish and trout should be considered within an order of magnitude since only two trout and one dogfish (Burger 1967) were used to calculate clearance. Further, different methods were used in determining these values in different species and the animals were in different nutritional states. Because of inherent limitations in the data obtained, few concrete conclusions can be drawn. However, the large differences in magnitude of the Tm, when calculated on a weight basis, have virtually disappeared. When Tm values are based on clearance values, no distinction in the ability to eliminate BSP exists among the fish and mammals included in Table 4. Extraction values listed previously for the dogfish, dog, and man also indicate functional similarities in dye excretion of the livers of fish and mammals. There is possibly a significant difference in the Tm clearance ratios of the trout when compared to those of the dogfish and rabbit.

The conclusions of Levine et al. (1971) concerning the limited ability of dogfish and mackerel to remove BSP must be reconsidered. If the Tm is the rate-limiting step of BSP removal in fish, and if the excretory processes involved in elimination of the dye are similar, then the data in Table 4 indicate a similar functional ability of fish and mammalian livers. The lack of BSP movement into the urine or across the gills in our limited analysis also supports this conclusion. Further, the results of Boyer (1971) support this conclusion.

The use of physiological rates as a base for comparing physiological processes between poikilothermic and homeothermic animals is suggested. Using a rate eliminates temperature effects and other associated problems. Comparative studies on the significance of rate differences could be more meaningful if the values were based on a standard physiological rate such as organ blood flow.

Our data suggest that rainbow trout remove the organic anion, BSP, more rapidly from the plasma than would be expected from information presented by other investigators for two other species of fish. In trout, as in mammals, the transport maximum of BSP into bile appears to be the rate-limiting step in the overall process of removal of BSP from blood to bile. A comparison of the Tm of BSP of two fishes with those of mammals, using the rate of clearance of BSP from the blood as the basis of comparison, indicates no difference between the excretory capacity of their respective livers.

Acknowledgments

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Coastal Movements of Mature Fraser River Pink Salmon (*Oncorhynchus gorbuscha*) as Revealed by Ultrasonic Tracking[1]

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STASKO, A. B., R. M. HORRALL, A. D. HASLER, AND D. STASKO. 1973. Coastal movements of mature Fraser River pink salmon (*Oncorhynchus gorbuscha*) as revealed by ultrasonic tracking. J. Fish. Res. Board Can. 30: 1309–1316.

Eleven mature pink salmon (*Oncorhynchus gorbuscha*) were tracked in September 1967 for periods of 3–50 hr over distances from 2 to 127 km to determine migration patterns.

The fish were classified as "active" or "passive." Active fish moved faster and their paths were straighter. Active tracks ended distant from and to the north (toward the Fraser River) of the release point; passive tracks ended near or south of the release point. Active fish did not follow shorelines, but travelled primarily along the axes of tidal currents. They moved both with the northward flood and against the southward ebb currents, during day and at night. Average ground speed of active fish was 62 cm/sec (2.2 km/hr).

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Nous avons suivi aux ultrasons les déplacements de saumons roses (*Oncorhynchus gorbuscha*) mûrs entre le détroit Juan de Fuca et le détroit de Georgie. Onze poissons ont été suivis de cette façon en septembre 1967, sur des périodes de 13 à 50 h et sur des distances de 2 à 127 km.

Les poissons se divisent en deux groupes: "actifs" et "passifs." Les poissons actifs se déplacent plus rapidement et leur route est plus droite que les autres. La piste des poissons actifs se termine plus loin et au nord (vers le fleuve Fraser) de l'endroit de mise en liberté; celle des poissons passifs s'arrête près et au sud de cet endroit. Les saumons actifs ne suivent pas la côte mais voyagent principalement dans l'axe des courants de marée. Ils se déplacent à la fois dans le même sens que le flux qui a une direction nord et contre le reflux qui a une direction sud, le jour aussi bien que la nuit. La vitesse moyenne, par rapport au fond, des poissons actifs est de 62 cm/sec (2.2 km/h).

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ALTHOUGH salmon make spectacular migrations, very little is known about their orientation mechanisms in the sea (Hasler 1966; Harden Jones 1968; Stasko 1971). Tagging–recapture studies with sense-impaired chum and Atlantic salmon in coastal waters have shown that olfaction plays an important role in reaching rivers, while vision (for chum salmon) does not (Hiyama et al. 1966; Bertmar and Toft 1969); results with olfactory impaired sockeye salmon (Craigie 1926) were inconclusive.

The general migration patterns of adult pink salmon (*Oncorhynchus gorbuscha*) have been studied by tagging–recapture of unimpaired fish in both open ocean (Neave 1964; Hartt 1966) and in coastal waters (Ward 1959; Vernon et al. 1964; Hourston et al. 1965; Neave 1966). Although the approximate routes and timing of the migrations are known, effects of the changing tidal currents, of daylight vs. darkness, and of the proximity of land on migratory movements cannot be studied by tagging–recapture techniques.

Tracking fish with ultrasonic transmitters provides a method to observe their migration patterns in greater detail (Stasko 1971). Coastal migration of several species of salmon has been studied by this technique (Hasler et al. 1970; Madison et al. 1972).

In this paper we report on migration patterns and deduced orientation mechanisms of pink salmon caught, tagged with ultrasonic transmitters, and released in the San Juan Archipelago (between the Strait of Juan de Fuca and Strait of Georgia)

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[1] This work is abstracted in Hasler et al. (1969b, 1970).

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some 70 km south of the Fraser River. The study was done in September (1967) when more than 95% of the adult pink salmon migrating through the San Juan Islands are destined for the Fraser River (Vernon et al. 1964; Hourston et al. 1965).

Methods

Most of the tracking was done in the protected waters of San Juan Channel which has its main stem in the south and two arms to the north (Fig. 1). The NW arm enters the Strait of Georgia through a gradually widening series of channels, while the NE arm narrows at Flat Point, then opens up into a bay from which several narrow passages provide access to the relatively open water of Rosario Strait (Fig. 3). Flood currents flow generally northward, ebb currents southward.

Mature pink salmon were captured with minimum trauma in a reef net (Anon. 1966). We selected the larger fish (approx. 3 kg); average total length was 64 cm (58.5–68.5 cm). We dipnetted them into either a box, for immediate transport to the release site, or into a holding cage. The cage was a wood-frame, wire-mesh cylinder, 1.8 m accross and 2 m deep, hung from an anchored raft.

Processing of the fish for release was similar to that described by Madison et al. (1972). No anesthetics were used. We released the fish either over the side of the boat directly into open water, or into a hoopnet from which they were allowed to swim out after 10–20 min observation. It took 0.3–1 hr to transport, process, and release a fish.

The two release sites (locations "b" and "d" in Fig. 1B) were 4 and 6 km from the capture site, and were located just outside and to the north of the commercial fishing boundary.

The ultrasonic transmitters, designed and constructed in our laboratory, were 7.6 × 2.2 cm cylinders weighing 50 g in water. The signal was continuous wave at 50 kHz with a usable signal range of 1.0–1.5 km.

Tracking was done from a 5-m outboard motorboat, except fish 1 which was tracked from an 11-m vessel. Tracking equipment and procedures after release of the fish were similar to those described by McCleave and Horrall (1970). Although presence of the boat appeared to have no effect on the fish (see also Johnson 1960; Hasler et al. 1969a; McCleave and Horrall 1970), we frequently altered our direction of approach to reduce the chance of biasing the fish's movements toward any particular direction.

During tracking we recorded sky conditions (sun, clouds, rain) and estimated wind speed and direction at hourly intervals. Rate and direction of boat-drift were measured by sextant fixes at start and end of drift period. Boat-drift as a measure of tidal currents in our study area was evaluated in September 1969. Three drogues (weighted crosswise metal vanes, 60 × 90 cm, suspended from a 30-cm diameter spherical float) were released simultaneously at 3, 10, and 30 m below the surface (Terhune 1968). A position fix was taken at the time of release. After 15–40 min the distance and direction from boat to nearest drogue were measured by compass and optical rangefinder; a position fix was again taken at one of the drogues, and the distances and directions from this drogue to the other two were measured.

The speeds of fish reported here, unless otherwise specified, are relative to ground; they are vector resultants of water currents and active locomotion by the fish. Vectors of approximate surface currents in Fig. 2 (dashed arrows) indicate distance the boat would have drifted in 30 min if the initial rate and direction of drift (measured over 5–20 min) were continued. Dotted arrows show direction of drift where speed was not determined. Straightness index, as used in Table 1, is defined as

$$\frac{\text{shortest water distance (start to end of track)}}{\text{length of fish's path}} \times 100$$

Results

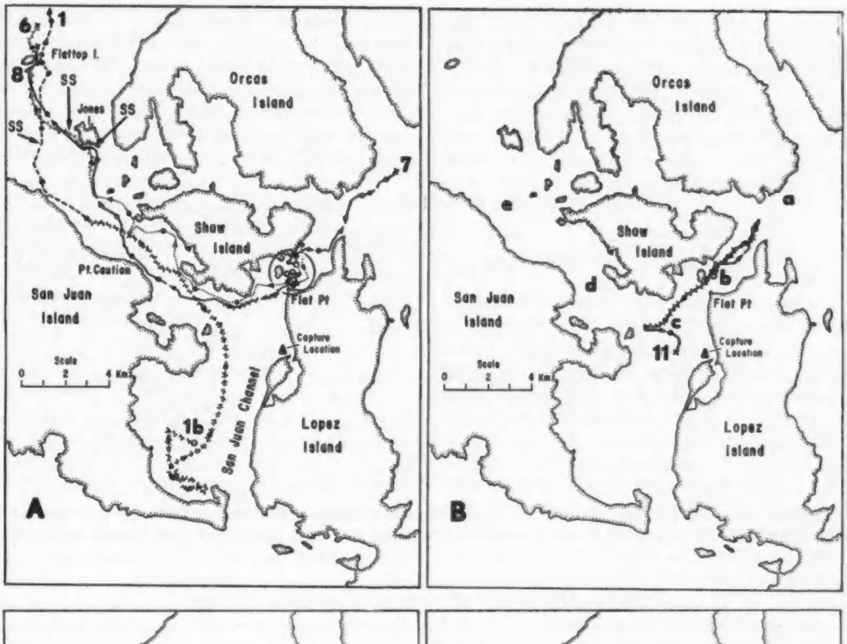
Eleven pink salmon were tracked (Fig. 1) for periods ranging from 3 to 50 hr for a total tracking time of 139 hr (Table 1). Length of individual tracks ranged from 2 to 127 km for a total of 293 km. Average ground speeds of individual fish ranged from 23 to 78 cm/sec. Winds during tracking were generally light. Strong winds over 18 km/hr (10 knots) during tracking lasted a total of only 4.2 hr, the longest period for a single track being 1.3 hr. Most tracking was done in light wind or calm (Table 1).

Most tracks were terminated in the evening. Only two fish (1 and 5) were tracked through the night. Track 1 was terminated when the signal became weak. Track 5 was terminated after movement had ceased for more than 1.5 hr in a fast current; presumably this fish either settled to the bottom or disgorged its transmitter.

WATER CURRENTS

In describing movements of the fish, allowance has to be made for passive transport by water currents (predominantly tidal in this area). The currents here are complex, especially at change of tide (slack water) with eddies in bays and temporary upwellings and undercurrents at junctions of channels. During peak currents, flows are more uniform, especially in midchannel.

Currents measured by 3-, 10-, and 30-m drogues were compared with boat-drift at five locations (Fig. 1B) with readings spaced through a full tidal cycle. Winds in all cases were light, less than 18 km/hr (10 knots). Currents measured at 3 m below surface (3-m currents) averaged 52 cm/sec (42 measurements). Average error in using boat-drift as an estimate of 3-m currents was 38%; the greatest errors were found at location "c" (44% average for 7 measurements). The error in


6
1
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Lopez Island
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Shaw Island
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Flat Pt
Capture Location
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Orcas Island
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4
San Juan Island
Flat Pt
Capture Location
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Lopez Island
D
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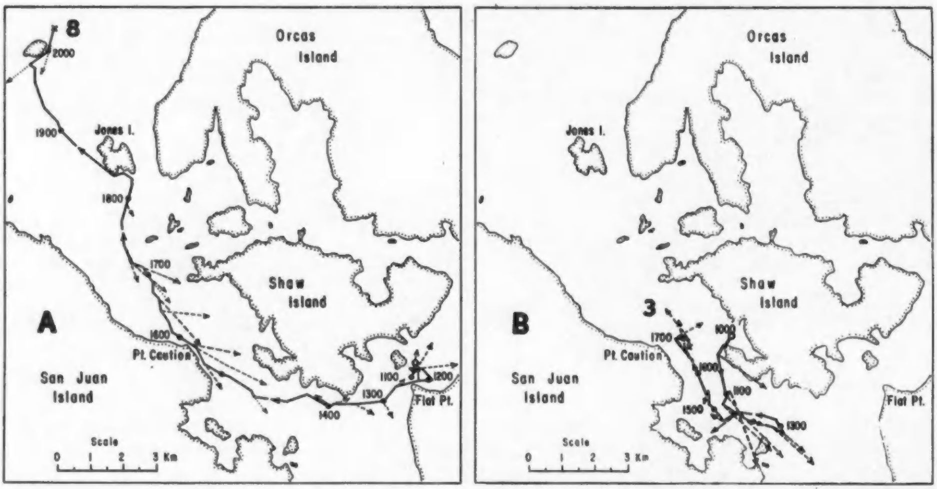
SR

FIG. 1. Paths of active fish (A) 1b, 6, 7, 8 and (B) 11; and of passive fish (C) la, 3, 10 and (D) 2, 4, 5, 9. Small open circles indicate start of tracking; "X" indicates end of tracking. Solid circles on paths mark hourly positions on the hour. "SS" and "SR" show locations of fish at sunset and sunrise. Hatch marks on each path indicate flood current (flowing northward); unhatched portions indicate ebb current (flowing southward); currents were not measured during track 7. Hatching is omitted inside large circle at Flat point (A). Letters in B show locations where we measured currents with drogues.


8
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A
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Pt. Caution
San Juan Island
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Flat Pt.
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Orcas Island
Jones I.
Shaw Island
3
B
1700
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Pt. Caution
1600
San Juan Island
1100
Flat Pt.
1500
1300
Scale
0 1 2 3 Km

FIG. 2. Sample of active (A) and passive (B) tracks. Dashed arrows are surface-current vectors; dotted arrows indicate direction only of current where speed of current was not recorded. Solid dots show hourly intervals.

TABLE 1. Quantitative description of individual tracks.

Track no.	Date track begins	Duration (*hr*)	Distance (*km*)	Avg ground speed (*cm/sec*)	Straightness index	% of time wind speed was 0–5 knots	Holding[a] time (*hr*)
1 (combined)	Sept. 1	50	127	71	36	81	23.5
			Active fish				
1b[b]	Sept. 2	32	86	75	58	83	–
6	Sept. 11	11	31	78	62	50	0.4
7	Sept. 12	5	8	45	78	94	0.6
8	Sept. 13	10	24	71	74	60	0.3
11	Sept. 16	10	15	40	26	74	92.4
Active fish	–	68	164	62	60	–	–
			Passive fish				
1a[b]	Sept. 1	18	41	71	21	77	23.5
2	Sept. 6	4	10	59	41	77	23.0
3	Sept. 7	8	11	41	12	17	2.7
4	Sept. 8	3	2	23	72	33	28.7
5	Sept. 9	25	40	45	30	90	47.8
9	Sept. 14	5	8	42	81	100	0.6
10	Sept. 15	8	17	56	29	87	73.5
Passive fish	–	71	129	48	41	–	–
All fish	–	139	293	52[c]	49[c]	–	–

[a] Time from capture to release.

[b] Division between active and passive sections of track 1 is seen by comparing Fig. 1a, 1c, and 3.

[c] The combined value for fish 1 was used in calculating the overall averages.

using boat-drift as a measure of current is least near peak currents (between changes of tide), and most at change of currents (slack water). The error is least for near-surface currents, most for deeper currents; average rate of separation between drifting boat and drogues (42 measurements) was 16 cm/sec for 3-m drogues and 29 cm/sec for the most distant 10- or 30-m drogue.

Lack of information on the swimming depth of individual fish and low accuracy of our current measurements preclude accurate description of the active component in movements of the salmon. Nevertheless, a qualitative evaluation of activity of each fish is meaningful.

ACTIVE VS. PASSIVE FISH

The 11 fish tracked were classified as active or passive (see Table 1 and Fig. 1) on the basis of movements relative to the drifting boat. Paths of six fish (2,3,4,5,9,10) and the first protion of track 1 (Fig. 1C and 1D) can be explained largely on the basis of passive drift with flood and ebb tidal currents. The others (Fig. 1A and 1B) cannot.

Active fish generally moved faster than passive fish relative to ground and their paths were straighter. The exceptions can easily be reconciled by considering the direction of travel in relation to direction of currents. Thus, the slow speed of active fish 11 is against the current while the fast speed of passive fish 1a, 2, and 10 is with the current in areas of fast currents. Similarly, the low straightness index of active fish 11 reflects its consistent movement against the current and reversal of direction during slack water, while the high straightness indices of passive fish 4 and 9 reflect their movement during only one phase of the current cycle.

Differences between tracks of active and passive fish are demonstrated in Fig. 2. Fish 8 (active) and fish 3 (passive) were chosen because more frequent current estimates (boat-drift) were available for these tracks. Both tracks are drawn on the same scale.

The active fish (Fig. 2A) moved irregularly for the first 1.5 hr after release, followed by consistent movement during the subsequent 8 hr up the NW arm of San Juan Channel. After the first 1.5 hr it moved against a flood current at Flat Point (ground speed of fish was 45 cm/sec), then through a change of current along the south shore of Shaw Island, followed by a long period of swimming against an ebb current (ground speed of fish was 68 cm/sec from Flat Point to Jones Island and 96 cm/sec beyond Jones Island).

The passive fish (Fig. 2B) moved generally in the direction of surface currents during both ebb and flood currents for the 8-hr duration of the track. Both temporary reversals of direction (at 1100 and 1700 hr), which did not follow the surface currents, occurred close to reefs.

All active tracks, except 11, ended distant from and to the north of the release point. All passive tracks ended near of south or the release point. In the study area salmon must move north to arrive at the Fraser River.

FACTORS AFFECTING ACTIVITY

Several factors were examined as possible causes for the differences in fish activity — for this purpose fish 1 is considered passive since it did not start active travel until 18 hr after release. The factors were (1) handling method at release (directly over side of boat vs. hoopnet), (2) size of fish, (3) presence or absence of commercial fishing nearby (as a possible factor in fragmenting schools of migrating salmon), (4) holding time from capture to release, and (5) spring vs. neap tides. Of these, only the handling method showed a significant difference when compared with fish activity ($p = .046$, Fisher exact probability test). However, handling method was closely related to advance of the season, as fish 1–5 (chronological order) were released via the hoopnet while fish 6–11 were released directly over the side. The p values of the other four factors were in excess of 0.18.

MOVEMENT PATTERNS OF ACTIVE FISH

Active fish, except fish 11 (and others only at beginning of tracks), maintained northerly courses within limits imposed by proximity of land during both flood and ebb. Apparent random movement occurred only at the start of tracks. Once they reached open water, such as was found beyond Jones Island, active fish moved almost due north (Fig. 1). Beyond Waldron Island, fish 1 still headed N (Fig. 3), as indicated by the direction of motoring while following the fish, though the SW ebb current produced a resultant path to WNW. When it reached open water beyond Saturna Island the fish continued in a N direction.

These salmon did not follow shorelines and did not enter bays or minor channels. In major channels, such as the NW arm of San Juan channel, active fish moved along the channel without reversing direction of movement when tidal currents reversed.

Two (fish 6 and 8) of three fish which passed Jones Island made landfall there, while all three fish (no. 1, 6, and 8) made landfall at Flattop Island despite different stages of tidal current when the fish passed (Fig. 1A).

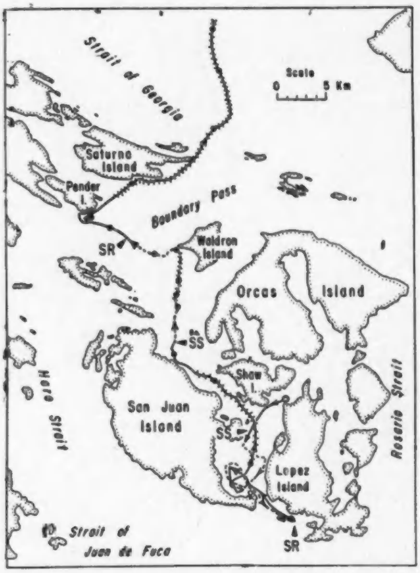

FIG. 3. Detail of longest track (fish 1). Solid line indicates daytime; dotted line indicates night. Hatch marks for flood currents are used only for active part of track. Solid circles on path indicate 2-hr intervals for active part of track. Symbols are same as in Fig. 1.

Swimming speed of fish relative to water could not be measured accurately because swimming depth was unknown. Therefore, detailed tabulation of swimming speeds is impossible. Maximum swimming speed relative to water was estimated for fish 8 in the region immediately north of Point Caution. This fish and location were selected because the fish was judged subjectively to be fast moving, the path was in open channel, currents were near peak speed, frequent boat-drift measurements were made during the track, and wind was light (less than 5 knots or 9 km/hr). Average ground speed over a distance of 3.9 km was 64 cm/sec against an average surface ebb current of 89 cm/sec (five boat-drift readings). Applying the correction for boat-drift as a measure of currents at location "e" (21 cm/sec), the active swimming speed was 64 + 89–21 = 132 cm/sec (4.75 km/hr). A comparable ground speed was shown by fish 6; it covered 13.2 km from the S tip of Shaw Island to Jones Island at an average speed of 93 cm/sec against an ebb current.

At night fish 1b traveled slowly (42 cm/sec average, in area of slow currents under overcast skies). By contrast, fish 6 and 8 traveled for 2.0 and 1.8 hr, respectively, past sunset (moonlit nights) with no apparent change in swimming speed or direction. The other two active fish were not tracked after sunset.

In the daytime, sunny conditions prevailed except during track 6 when sun was intermittently obscured by clouds. This had no apparent effect on movements of fish 6.

Discussion

Passive fish are of little value in studies of fish migratory movements, if such behavior is not normal at the time and place of the study. Tagging and recapture studies indicate no delay for adult pink salmon migrating through the San Juan Islands (Vernon et al. 1964; Hourston et al. 1965). Presumably the passive behavior of some of our fish was an experimental artifact.

Handling of the fish at release (observation in hoopnet prior to release) and/or seasonal differences appear to influence activity of the fish. Possibly after prolonged tracking the passive fish would have regained normal activity, as happened with fish 1 after 18 hr of tracking. Another factor which may have affected activity was the weight of the transmitter (50 g in water). Similar transmitters used in Fraser River sockeye salmon also resulted in many passive fish. Passive sockeye were rare when smaller transmitters (18.5 g in water) were used near the Fraser River (A. B. Stasko et al. unpublished data) and Skeena River (Madison et al. 1972).

Once our fish started moving actively, their behavior was assumed to be representative of free-swimming pink salmon in this area. This assumption is supported indirectly by similarities in speeds of our fish and speeds of pink salmon studied by other techniques. Tagging–recapture studies have shown that pink salmon in this area average 46 cm/sec assuming straight courses (Vernon et al. 1964); average ground speed of our active fish (62 cm/sec) is comparable, since actual paths are not necessarily the shortest routes. Ocean tagging of pink salmon has yielded travel speeds of 50–69 cm/sec (43–60 km/day) over distances up to 2000 km (Hartt 1966).

The average ground speed of our active pink salmon (62 cm/sec for fish of 58.5–68.5 cm total length) is similar to the metabolically most efficient speed of adult sockeye salmon (55 cm/sec for 55-cm fish; Brett 1965) and the 53 cm/sec average speed of ultrasonic-tracked sockeye salmon in coastal waters near the Skeena River (Madison et al. 1972). The fastest observed swimming speed of our pink salmon (132 cm/sec for the 65-cm fish, or 2.0 body lengths/sec) is less than the maximum 60-min sustained swimming speed of a 65-cm sockeye salmon at 14 C (180 cm/sec, or 2.8 body lengths/sec; Brett and Glass 1973).

Pink salmon in the San Juan study area apparently swim close to surface as indicated by catches mostly in the top few meters of gillnets, by salmon frequently jumping above the water surface, and by the very nature of reef nets which depend on fish swimming within a few meters of the surface. Twice during track no. 7 we were able to see our tagged fish (yellow external tag) swimming 2–3 m below the surface.

A consistent aspect of migratory movements of the active fish was general straightness of path along the axes of major tidal currents despite an irregular shoreline. Possible mechanisms for maintaining such movement patterns include ability to detect presence of land at distances greater than underwater vision, or ability to orient to electric fields generated by water currents. Atlantic salmon and American eels can detect such weak electric fields (Rommel and McCleave 1973). The water-current-generated electric fields contain information on speed, axis, and direction of water currents (Royce et al. 1968) and are independent of diurnal factors.

Movement of active fish in a generally northward direction indicates an additional compass-related direction sense(s) functional both day and night. As in the case of cutthroat trout (McCleave and Horrall 1970; McCleave and LaBar 1972) and sockeye smolts (Groot 1965), one is tempted to postulate directional cues such as magnetic compass or celestial–visual cues. One can also postulate use of gradients in water quality. In our study area the influence of Fraser River can be detected as reduced salinity and increased temperature and turbidity (Herlinveaux and Tully 1961; Waldichuk 1957).

The migration patterns of our active pink salmon in relation to water currents, but independent of water-current reversals, differ from observations on other species tracked close to or in the lower (tidal) part of their home rivers. Close to (American shad, Leggett 1973) and in their home rivers (coho salmon, Scholz et al. 1972; Atlantic salmon, Stasko et al. 1973), anadromous fish appear to progress upriver by stemming ebb currents and by holding positions on flood currents. One can hypothesize that pink salmon also will show such a differential response to ebb and flood currents when swimming closer to or in the tidal part of their home river.

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Coupling Carbon Flow Through Some Pelagic and Benthic Communities[1]

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Sediment core oxygen uptake is correlated positively with primary production and inversely with mixed-layer depth in various aquatic ecosystems for which the input of organic matter is predominantly autochthonous. In these areas organic carbon sedimentation is proportional to the ratio of carbon input: mixed-layer depth, which reflects increased mineralization with increased depth of mixing. The ratio of primary production: mixed-layer depth is compared with the carbon equivalent of oxygen uptake by sediments to derive an expression which is used to calculate the amount of photosynthetically fixed carbon respired at the sediment surface.

HARGRAVE, B. T. 1973. Coupling carbon flow through some pelagic and benthic communities. J. Fish. Res. Board Can. 30: 1317–1326.

L'absorption d'oxygène dans une carotte de sédiment est en corrélation positive avec la production primaire et en corrélation inverse avec la profondeur de la couche mélangée, dans divers écosystèmes aquatiques dans lesquels l'apport de matière organique est avant tout autochtone. Dans ces régions, la sédimentation du carbone organique est proportionnelle au rapport entrée du carbone: profondeur de la couche mélangée, réflétant une minéralisation qui augmente en fonction de la profondeur du mélange. Nous comparons le rapport production primaire: profondeur de la couche mélangée avec l'équivalent en carbone de l'absorption d'oxygène par les sédiments afin d'établir une formule qui est utilisée dans le calcul de la quantité de carbone fixé par photosynthèse respiré à la surface des sédiments.

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SEDIMENTS underlie all natural aquatic communities and events at the mud–water interface might be expected to reflect processes of production and mineralization within the water column. Sediments have been thought to indicate lake type (Naumann 1932), and Hansen (1961) attempted to quantify a relationship by comparing C/N, organic matter, silica, and $CaCO_3$ in the sediments of several Danish lakes. He demonstrated that oligotrophic lakes contained sediments of inorganic minerals and organic detritus while sediments in eutrophic lakes were derived mainly from plankton. Unfortunately it was not possible to compare these analyses with measures of primary production. No simple chemical characteristics of sediment have been found which can be used as indicators of water body productivity (Hayes 1964), but a positive correlation between fish catch and oxygen uptake by lake sediments has been established (Hayes and MacAulay 1959). Rybak (1969) also used sediment oxygen consumption to rank various Polish lakes of different trophic type, but no quantitative measure of productivity was given.

The present study demonstrates that of oxidizable organic matter input to certain aquatic ecosystems can be quantified by measuring oxygen uptake across an undisturbed sediment-water interface. I have measured sediment core oxygen uptake in various freshwater and marine environments which receive organic matter derived predominantly from photosynthesis for which annual estimates of primary production were available. These data, supplemented with similar measurements made by other workers, are used to fit the expression:

$$C_o = a\,\frac{(C_i)^b}{(Z_m)^c}$$

where C_o = carbon equivalent of sediment oxygen uptake (g C m^{-2} $year^{-1}$)
C_i = annual primary production (g C m^{-2} $year^{-1}$)
Z_m = mixed-layer depth (m)
a, b, c = constants

The expression is used to fit model curves relating carbon utilization by bottom communities to carbon supply.

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[1] Bedford Institute of Oceanography Contribution.

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TABLE 1. Comparison of primary production and sediment core oxygen uptake in various areas. All values are estimated annual means except for data in references 1, 2a, and 2b which are derived from single visits.

Ref.[a] no.	Location	Total depth (*m*)	Mean mixed–layer depth (*m*)	Temp. (*C*)	Primary production (g C m^{-2} year^{-1})	Sediment oxygen uptake (l O_2 m^{-2} year^{-1})
1.	Woods Hole	15	15	7	120	88
	(offshore)	1850	75	4	120	4
2a.	Eastern	85	85	15	300	38
	Tropical	275	200	15	300	33
	Pacific	1325	250	15	300	6
	(off	2820	250	15	300	36
	Peru)	2900	250	15	300	16
2b.	Northeastern Pacific	125	30	7	62	41
	(off Oregon)	2750	100	7	62	15
3.	Long Island Sound	20	20	10	205	179
4.	Puget Sound					
	stn. 1	9	9	12	275	184
	stn. 18	196	196	10	460	88
5.	Lawrence Lake	12	5	5	169	257
6.	St. Margaret's Bay	60	20	3	792	298
7.	Tuel Lake	17	6	8	595	385
8.	Bagsvaerd Lake	2	2	10	522	429
9.	Frederiksborg Castle Lake	3	3	10	580	377
10.	Fure Lake	38	26	7	310	219
11.	Lake Esrom	20	10	6	191	175
12.	Grane Lang Lake	11	11	11	153	81

[a]References and comments (Table 1): All measures of primary production are assumed to represent net measures of carbon fixation:

1. Primary production (^{14}C) from Ryther (1963) off Massachusetts coast. Average of summer and winter values of sediment core oxygen uptake in shallow water (Kanwisher 1962) and of 10 single in situ measurements under bell jars at 1850 m (Smith and Teal 1973). Complete mixing assumed in shallow water. Thermocline depth offshore varies between 50 and 100 m (K. L. Smith personal communication).

2a. Primary production (^{14}C) in Peruvian coastal water (eastern tropical Pacific) from Ryther (1969). Sediment core oxygen uptake measured at 15 C, mean of duplicate determinations made with cores from various depths (Pamatmat 1971a).

2b. Primary production (^{14}C) for Washington and Oregon coasts from Anderson (1964). Sediment core oxygen uptake measured at 7 C, mean of duplicate cores from various depths (Pamatmat 1971a). Mixed-layer depths discussed by Anderson (1964).

3. Net primary production (light–dark bottle oxygen method) in Long Island Sound from Riley (1956). Carey's (1967) measure of sediment core oxygen uptake based on nine determinations (paired cores) made at various times of the year expressed as a weighted average to compensate for paucity of winter and fall data. Tidal currents prevent stratification in Long Island Sound.

4. Primary production (^{14}C) at station I and II Puget Sound, Washington (Pamatmat and Banse 1969). Estimated annual oxygen uptake based on five quarterly visits (Pamatmat 1971b). Replicate (3–4) cores incubated at various temperatures. Tidal flushing prevents stratification. Shallow (stn. 1) and deep (stn. 18) sample stations near locations near localities of primary production measurements.

5. Primary production in Lawrence Lake, Michigan, taken as the sum of carbon fixation by macrophytes, epiphytes, and phytoplankton (Wetzel et al. 1972). Sediment core respiration measured directly as CO_2 production derived from measurements throughout the year at various depths, converted to oxygen equivalents by assuming R.Q. = 0.85.

6. Total primary production in St. Margaret's Bay, N.S., taken as the sum of primary production by phytoplankton (^{14}C) (Platt 1971) and littoral seaweed (Mann 1972). Sediment core oxygen uptake from triplicate samples taken during winter, spring, summer and fall. Mixed-layer depth estimated as average thermocline depth.

7–12. Primary production measurements (^{14}C, light-dark bottle oxygen method) summarized for various Danish lakes by Whiteside (1970). Measurement of sediment core oxygen uptake is an average of at least three determinations (duplicate cores) over summer and winter seasons, as described for Lake Esrom (Hargrave 1971).

Methods

Undisturbed sediment cores (10–15 cm long) were taken with overlying water (300–500 ml) using a Kajak corer, described by Brinkhurst et al. (1969). A ring support ensured perpendicular penetration and allowed coring tubes to be only half-filled with sediment. The sediment was usually soft mud or clay which the corer penetrated easily. At least three cores were taken on each sampling occasion. Sampling dates were chosen so as to allow an estimate of the annual mean rate of oxygen uptake by the sediments; in some areas visits were made once a month for a full year, but in other locations samples were obtained only during each season. Sampling frequency and location are summarized in Table 1.

Cores were usually taken from sediments near the center of a water body. Primary production is probably the major carbon source in all the areas considered; it is assumed here that contributions of organic material from littoral areas, shores, or inlet streams do not materially affect the carbon budgets of these systems.

Measurements of oxygen uptake by the sediment cores began usually 1 hr after collection, with the exception of cores from Grane Lang Lake which were transported overnight and used the following day. Temperature change was minimized but fluctuations of up to 5 C may have occurred before cores were incubated in the dark in a constant temperature chamber preset to the collection temperature. Magnetic stirrers mounted in stoppers provided an airtight seal on the top of the cores after initial samples were taken for measurement of dissolved oxygen. Stirring prevented the formation of artificial gradients of oxygen concentration within the water column. Either a micro-Winkler method (Hargrave 1969a) or a Radiometer Blood Gas Analyzer was used to determine changes in dissolved oxygen in water over sediment cores during the next 6 hr. Water taken from above the sediment and placed in BOD bottles showed no change in dissolved oxygen during 6 hr and all oxygen consumption in cores was therefore assumed to be due to uptake at the sediment surface.

Primary production is usually measured as organic carbon and for comparative purposes the carbon equivalent of sediment oxygen uptake was calculated assuming an R.Q. = 0.85[2]. The choice of a value of 0.70 or 1.0 would alter calculations by ± 17%. R.Q. values for salt marsh (Teal and Kanwisher 1961) and intertidal sandflat (Pamatmat 1968) sediments range from 0.27 to 0.96. Pamatmat (1971b) assumed an R.Q. of 1.0 in calculating the carbon equivalent of sediment oxygen uptake in Puget Sound. This value is unlikely to be the same in different communities and it might change seasonally as the proportion of chemical oxidation and biological respiration is altered. No measures of R.Q. values exist for the sediments used in this study and there is no alternative to the general use of a common value if data on oxygen uptake are to be expressed in terms of carbon flux. Even if absolute values thus calculated are in error, all data have been converted by the same factor and comparison on a relative basis still seems justified.

Results

A step-wise multiple linear regression was used to evaluate the effects of total water column depth, mixed-layer depth, temperature at the sediment surface, and carbon supply (primary production) on oxygen uptake by sediment cores from various lakes, bays, and coastal areas for which mean annual estimates are available (Table 1). Logarithmic transformation of all variables improved the regression which showed only mixed-layer depth and primary production to be significantly ($P < 0.05$) related to oxygen uptake by sediment cores (Table 2).

Both total water column depth and mixed-layer depth were negatively correlated with oxygen uptake by sediments but these variables themselves showed a significant positive correlation ($r = 0.93$) (Table 2). This probably accounts for entry of mixed-layer depth in the multiple regression, while total water column depth was not significantly correlated. Mean annual temperature was not significantly correlated with any other variable.

From the equation derived in Table 2, oxygen uptake (C_o) by these sediment surfaces can be described by,

$$C_o = a(C_i)^b (Z_m)^{-c} \qquad (1)$$

where C_o is calculated from the combined effects of primary production (C_i) and mixed-layer depth (Z_m). Since the correlation with mixed-layer depth is negative, the expression becomes,

$$C_o = a \frac{(C_i)^b}{(Z_m)^c} \qquad (2)$$

The slope coefficients b (0.51) and c (0.36) derived from the multiple regression are significantly

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[2] M. Pamatmat (personal communication) suggests that chemoautotrophic metabolism, which normally occurs in sediments, would lower the R.Q. below 0.7. A mean value of 0.6 can be derived from data of Teal and Kanwisher and Pamatmat.

Mixed-layer depth taken as average thermocline depth during spring and summer except in those lakes (8, 9, 12) which do not stratify.

Primary production in Grane Lang Lake calculated from the sum of production by phytoplankton (Whiteside 1970) (80 g C m^{-2} $year^{-1}$) and bottom vegetation (Nygaard 1958) (73 g C m^{-2} $year^{-1}$). Nygaard's measurements of net oxygen production by *Nitella* and *Nostoc* estimated to represent a daily biomass increment on an annual basis of 0.5% of a mean standing stock of 40 g C m^{-2}.

TABLE 2. Step-wise multiple linear regression analysis of $\log_{10}$ transformed data (Table 1) excluding data in references 1, 2a, and 2b. Total water column depth (X_1), mixed-layer depth (X_2), temperature (X_3), and annual primary production (X_4) compared with annual sediment oxygen uptake (Y).

	Correlation matrix				
	X_1	X_2	X_3	X_4	Y
X_1	1	.93	−.37	−.12	−.59
X_2	.93	1	−.06	−.23	−.78
X_3	−.37	−.06	1	−.26	−.33
X_4	−.12	−.23	−.26	1	.60
Y	−.59	−.78	−.33	.60	1

Iteration no.		Slope coefficient	SD	T-ratio	MR²
1	constant	209			
2	constant	566			
	X_2	−0.41	0.11	3.69	0.61
3	constant	26.7			
	X_2	−0.36	0.09	4.06	
	X_4	0.51	0.19	2.68	0.87

different (Table 2) and the equation cannot be further simplified. However, since primary production and mixed-layer depth are both independently related to sediment oxygen uptake, a single expression

$$C_o = a_2 \left(\frac{C_t}{Z_m}\right)^{b_2} \tag{3}$$

may be derived. This equation allows all three variables to be plotted on a single graph which shows a positive logarithmic correlation between sediment oxygen uptake and the ratio of primary production: mixed-layer depth (Fig. 1). Sediment oxygen uptake is thus expressed as a function of carbon supply to the bottom.

Data from areas for which annual estimates of sediment oxygen uptake are not available have not been included in the regression analyses (Fig. 1, Table 2) but for comparison these individual measurements, expressed on a yearly basis (Table 1), are plotted in Fig. 1. The ratio of primary production: mixed-layer depth for each of these measurements is less than 10 and all values are less than would be predicted from an extrapolation of the calculated regression line.

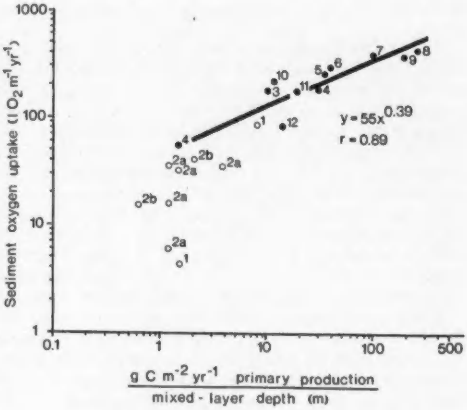

FIG. 1. Comparison of sediment oxygen uptake and the ratio of carbon fixed during primary production: mixed-layer in various freshwater and marine areas. Regression line calculated omitting data (open circles) from those areas (1, 2a, 2b) where annual estimates of production and oxygen uptake cannot be made.

Different values for annual primary production and mixed-layer depth can be substituted in equation (2) and the annual rate of sediment oxygen uptake calculated. These values, expressed in terms of carbon loss at the sediment surface by multiplying by 0.456 (R.Q. = 0.85), can be compared directly with carbon fixed during photosynthesis for different mixed-layer depths (Fig. 2). It must be emphasized that the absolute amounts of carbon lost depend on actual R.Q. values. For comparison, however, these estimates can be expressed as a percent of carbon fixed during photosynthesis and the percent of primary production metabolized at the sediment surface calculated (Fig. 3).

As primary production increases for any depth of mixing, the absolute amount of carbon lost across the sediment surface increases (Fig. 2), but the percentage of the production removed at the sediment surface decreases (Fig. 3). Pelagic communities thus become increasingly important in oxidizing organic matter as either primary production or mixed-layer depth increase. Conversely, at low rates of primary production, while bottom communities receive reduced amounts of carbon, the percentage of photosynthetically fixed carbon dissipated increases with decreasing primary production or depth of mixing. The greatest change in the proportion of primary production oxidized at the sediment surface occurs at low levels of primary production with shallow mixed-layer depths. At high rates of primary production, while the absolute amount of carbon removed at the sediment is high, it remains approximately constant in proportion to phytoplankton carbon supply.

Discussion

Interest in predicting the productive capacity of a body of water dates from the classical attempts of Thienemann (1928) and Naumann (1932) to classify lakes as to "trophic" type. These earlier comparisons of lakes were based largely on the standing stocks of nutrients, morphometry, or type of bottom fauna and suffered from the lack of any quantitative measure of production. Rawson's (1955) comparison of fish catch in large Canadian lakes established a quantitative relation between morphometry (mean depth) and fish yield, taken as an index to lake productivity. Other attempts to relate fish catch to various factors such as alkalinity or total dissolved solids, however, were not successful (Ball 1945; Northcote and Larkin 1956 and Hayes 1963).

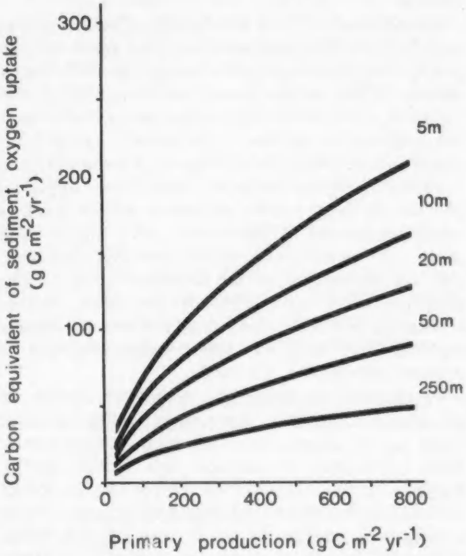

FIG. 2. Model curves calculated from multiple regression (Table 2) relating the carbon equivalent of sediment oxygen uptake to different levels of primary production and mixed-layer depth.

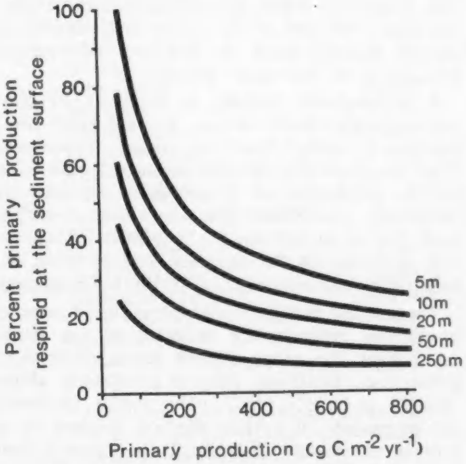

FIG. 3. Carbon equivalent of sediment oxygen uptake, (Fig. 2) expressed as a percent of primary production for various values of production and mixed-layer depth.

Measurements of primary production by ^{14}C techniques have often received criticism and have been shown to underestimate organic production determined simultaneously by alternate methods (Ryther et al. 1970; Sutcliffe et al. 1970; Morris et al. 1971). Despite these criticisms, ^{14}C uptake has come to be used as a standard method for measuring phytoplankton production and even if it is useful only as a relative index it does provide some measure of the productive capacity of an aquatic community. The present study supports Hayes' and MacAulay's (1959) observation that sediment oxygen uptake is related to the productivity of a water body. Apparently both primary production and fish yield can be related to oxygen consumption by undisturbed sediment surfaces.

Oxygen uptake by sediment can be expected to index primary production only in areas not receiving allochthonous organic material. In Lake Windermere North Basin, for example, only a small proportion of the total carbon respired and buried in the sediment could be supplied by phytoplankton production (Lund et al. 1963). Similarly the comparison is not applicable to rivers or lakes with high flushing rates where allochthonous particulate and dissolved carbon sources contribute substantially to the carbon budget.

Two areas considered in this study, Puget Sound and Bagsværd Lake, receive organic matter in the form of sewage discharge, but oxygen consumption by sediment cores from these areas corrected for differences in mixed-layer depth and primary production (Fig. 1), show little indication of this enrichment. Macrophytes and emergent vegetation occur in littoral areas of all lakes considered in the present study, but carbon input from these sources is not thought to be important in terms of that supplied by phytoplankton. Hansen (1961) concludes that sediments in oligotrophic Grane Lang Lake are derived chiefly from benthic vegetation, while sediments in more eutrophic Danish lakes are produced from a planktonic supply.

Annual seaweed production in littoral areas of St. Margaret's Bay is three times greater than phytoplankton production (Platt 1971; Mann 1972). While some of this organic matter may be lost in dissolved form or through flushing to offshore areas, studies of seasonal changes in C/N in suspended (Sutcliffe 1972) and sedimented (M. Paranjape unpublished data) material suggest that a significant part of the organic matter supplied to deep sediments is derived from products of seaweed decomposition. Increased rates of oxygen uptake by sediment cores during winter, when seaweed production is high and phytoplankton production is low, coincide with high rates of sedimentation, demonstrating the importance of this carbon supply to the sediment.

In a previous study I observed a significant positive logarithmic correlation between oxygen uptake by sediment cores and temperature during experiments performed over an annual period (Hargrave 1969b). A similar relation existed for individual measurements made in various areas during the present study, but on a mean annual basis there was a nonsignificant negative correlation (Table 2). This might reflect the narrow temperature range represented in the present data. It might also show, however, that on an annual basis bottom community metabolism is more dependent on organic matter supply, a function of depth, than on mean temperature. Pamatmat and Banse (1969) noted that temperature changes only explained 30% of the total variation in sediment oxygen uptake in Puget Sound and they also suggest that a large part of the unexplained variance may be due to varying rates of supply of organic matter.

When organic matter arrives at a sediment-water interface it may be oxidized, buried, and partially consumed by anaerobic metabolic processes, or accumulated as fossilized organic compounds (see Pamatmat 1971a). Loss of sediment carbon as organisms through predation or emergence may also be a significant pathway of carbon removal from some bottom communities. Estimates of fossilization, however, are available for comparison with carbon supply in various areas (Table 3).

Organic carbon accumulation in sediments is less than 10% of the total annual supply to the ecosystem in all areas except those where sediment is partly terrigenous in nature. Thus, in areas which receive primarily autochthonous organic matter, decomposition at the sediment surface reflects directly the supply of organic substances not oxidized in the water column. The positive logarithmic relation between sediment oxygen uptake and primary production per unit mixed volume (Fig. 1) supports this idea and confirms Ohle's (1956) observations on north German lakes. Organic carbon sedimentation is proportional to the ratio of carbon input: mixed-layer depth, which reflects increased mineralization with increased depth of mixing.

Kleerekopper (1953), Ohle (1965), Ławacz (1969), and Riley (1970) also conclude that most decomposition occurs in the upper mixed-layer of a water column. This would provide an explanation for the reduced rates of oxygen uptake by deep water sediments with primary production: mixed-layer depth ratios of less than 10 (Fig. 1). If mineralization is almost complete within a mixed-layer depth of 50–100 m, deep water sediments receive such a small proportion of the total carbon supply that there may be no clear relation between this input and decomposition at the sediment surface. The comparison is made difficult for deep oceanic sediments, however, which may not receive organic material from overlying water where measures of primary production are made.

Productivity in lakes has long been known to be related to depth. Thienemann (1928) classified lakes as to trophic type by their morphometric ratio of volume to surface area (mean depth). Rawson (1955), Ohle (1956), Hayes (1957), Ryder (1965), and Schindler (1971) have all related various productivity indices to an inverse of this ratio. Generally, in all of these comparisons, as mean depth increases, indices of production decrease. Larkin (1964), in reviewing Rawson's work, suggests some reasons for the effect of depth on production in large lakes. The present study supports his idea that increased depth of mixing, which usually increases with size of the water body, results in greater decomposition of products of primary production in the water column.

A proportional decrease in oxidation of photosynthetically fixed carbon by sediment communities at higher levels of primary production (Fig. 3) supports the view that during eutrophication benthic production is progressively replaced by planktonic production. The main effect of enrichment may be to decrease the proportion of respiration occurring at the sediment surface while enhancing oxygen consumption in the water column.

The greatest changes in the proportion of primary production reaching the sediment at any depth occur over the range of low levels of primary production. Doubling primary production above 200–300 g C m^{-2} $year^{-1}$ only slightly decreases the percentage of that production respired by a bottom community (Fig. 3). Thus, primary production in oligotrophic waters is less efficiently utilized by pelagic communities and the lower the primary production the larger the proportion which reaches the sediments. It must be emphasized that this observation is based on annual averages from different areas and in any one location seasonal differences may occur between peaks in primary production and decomposition at the sediment surface (Hargrave 1971). This contrasts, however, Margalef's (1968) suggestion that plankton in eutrophic waters contribute relatively more to the sediment. While the absolute carbon input to sediments increases with increasing primary production (Fig. 2), the percent metabolized at the sediment surface decreases (Fig. 3). Perhaps this reflects the inability of planktonic communities, primarily zooplankton, to fully exploit dilute populations of small algae which characterize oligotrophic conditions (Margalef 1968).

Few previous studies have related energy flow through bottom communities to pelagic primary production. Jónasson (1964) demonstrated that *Chironomus* larvae in Lake Esrom profundal mud grow well only during short periods of the year when mixing supplies freshly produced organic material to the sediment surface. Measures of oxygen uptake by sediment cores from central Lake Esrom also show maxima during spring and fall which correspond to periods of *Chironomus* growth (Hargrave 1971). A 2-week delay between peaks in primary production and increased oxygen consumption at the mud surface may indicate the length of time required for products of primary production not consumed in the water column to reach the sediment.

Hall et al. (1970) compared the ratio of zooplankton and benthos production in small ponds under various conditions of nutrient enrichment and fish predation. The ratios averaged slightly greater than unity over 3 years even though production in both communities varied in response to fertilization. Changes in zooplankton production were balanced by equal changes in production

TABLE 3. Comparison of the fate of organic carbon in various aquatic ecosystems.

Location and reference	Depth (*m*)	% of carbon supply lost Water column	 Sediment surface	 Fossilized	 Transported
Barents Sea	200–300	(——— 93	———)	7	
Caspian Sea	950	(——— 94	———)	6	
Black Sea	2200	(——— 94	———)	6	
Hayes (1964)					
Lake Washington Edmondson (1966)	60	71	27[a]	2[b]	–
Marion Lake Hargrave (1969a)	5	No estimate	27	4	69
Sargasso Sea Riley (1970)	4000	99.5	0.4	<0.1	–
Black Sea Deuser (1971)	2200	80–95	5–10	4	3
Chesapeake Bay	5	43	28[c]	27	2
Biggs and Flemer (1971)	15	61	10[c]	10	19
Bay of Quinte	5	No estimate	23[e]	77[e]	No estimate
Johnson and Brinkhurst (1971)	30	No estimate	91[e]	9[e]	No estimate
Lake Esrom Hargrave (1971)	20	66	33	1[d]	–
Hubbards Brook Fisher and Likens (1972)	Shallow pools and riffles	(——— 34	———)[e]	–	66
Lawrence Lake Wetzel et al. (1972)	12	27.8	56.8	7.1	1.4

[a] Estimated from hypolimnetic oxygen deficit.

[b] Calculated assuming sediment accumulation as 2 mm year^{-1}.

[c] Estimate by difference.

[d] Sediment accumulation 0.57 mm year^{-1} (Whiteside 1970).

[e] Energy equivalent of sediment oxygen uptake as a proportion of energy content of sedimenting material.

of bottom fauna. Rowe (1971) correlated biomass of bottom fauna in several oceanic areas with depth and primary production. The amount of animal biomass was related to the magnitude of primary production and the decrease in biomass with increasing depth was a function of the rate of change in primary production from shallow to deep offshore water. Both studies demonstrate that energy flow through planktonic and bottom communities can be closely linked.

Johnson and Brinkhurst (1971) constructed annual energy flow diagrams for benthic communities in four different areas of the Bay of Quinte, Lake Ontario. Macroinvertebrate production was compared with energy input (sedimentation) and energy flow through the total bottom community (oxygen uptake by sediment cores). At the inner bay station, where terrestrial debris probably contributed substantially to sediments, the energy equivalent of sediment oxygen uptake was 23% of the measured energy input through sedimentation. Macroinvertebrates assimilated only 2% of this supply. At lakeward stations, however, 90% of the sedimented organic matter was metabolized and macroinvertebrate assimilation amounted to 30% of the supply.

Johnson and Brinkhurst (1971) did not observe a direct proportionality between sedimentation and sediment oxygen uptake since oxygen consumption by sediment cores from the inner bay did not reflect extremely high sedimentation in that area. Sediment accumulation was also maximum at this station, indicative of inefficient metabolism of the carbon supply. At other stations, however, where terrestrial debris may have contributed less to sediments, both sedimentation and bottom community metabolism were of the same order of magnitude.

Comparisons between production and mineralization in various shallow water environments show that pathways by which organic carbon is lost depend on mechanisms of supply. In rivers and shallow ponds which receive terrestrial debris, mineralization is not complete and organic carbon may be transported or buried (Uyeno 1966). In other areas with lower input of terrigenous organic matter there may be a close dependence between primary production and decomposition in the water column and at the sediment surface (Seki 1967; Marshall 1970).

Pelagic communities may serve as filters to the passage of organic matter to sediments. Carey (1972) observed a rapid decrease in concentration of Zn^{65} in both asteroids and sediments with increasing depth off the Oregon coast. Concentrations declined fairly constantly with distance from the mouth of the Columbia River, however, perhaps due to reduced mixing in the less saline plume area. Similar patterns of distribution may be found for pesticides in aquatic ecosystems. The lipophilic nature of these residues results in a close association with particulate matter which increases their availability to filter-feeding invertebrates and provides direct access to lipid pools in other organisms through food-chain transfer. Insofar as the concentration of suspended particulate material in the euphotic zone is directly related to primary production, the fate of these contaminants may be closely associated with natural cycles of organic matter. Thus, the relationship described here for carbon flux between pelagic and bottom communities may also apply to the transfer of contaminants from the water column to the sediments.

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Gastric Digestion, Food Consumption, Feeding Periodicity, and Food Conversion Efficiency in Walleye (*Stizostedion vitreum vitreum*)[1]

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SWENSON, W. A., AND L. L. SMITH JR. 1973. Gastric digestion, food consumption, feeding periodicity, and food conversion efficiency in walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 30: 1327–1336.

Gastric digestion of walleye, *Stizostedion vitreum vitreum*, and sauger, *Stizostedion canadense*, was measured by pumping stomachs at various intervals after experimental meals had been force-fed or voluntarily consumed. No significant differences in digestion rates were found between species or among walleye taken from three lakes. Repeated use of fish in digestion experiments failed to influence results. Gastric digestion rate increased with fish size, but was depressed by increased meal size, food particle size, and by force-feeding experimental meals.

Food consumption rate and feeding chronology of the strong 1966 year-class of Lake of the Woods walleye were determined by applying results of laboratory digestion studies to stomach samples. An estimating technique that takes into account the effects of factors shown to influence digestion in the laboratory was developed and used to make calculations for the field population. Consumption averaged 1% of body weight during June, 2% during July, and 3% during August and September. Average temperatures were similar during June and September. Greater consumption during September resulted from higher food availability. Feeding was greatest during night and early morning hours in all months except June when it was continuous. Conversion efficiency of the 1966 year-class was described from estimates of growth and consumption rates for June through September and approximated 20% during each month.

SWENSON, W. A., AND L. L. SMITH JR. 1973. Gastric digestion, food consumption, feeding periodicity, and food conversion efficiency in walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 30: 1327–1336.

Nous avons mesuré la digestion gastrique chez le doré jaune, *Stizostedion vitreum vitreum*, et le doré noir, *Stizostedion canadense*, en pompant les estomacs à divers intervalles après gavage ou consommation volontaire de repas expérimentaux. Nous n'avons pu déceler de différences interspécifiques ou entre les dorés provenant de trois lacs. Le fait de soumettre les mêmes poissons à des essais répétés n'affecte pas les résultats. Le taux de digestion gastrique augmente en fonction de la taille du poisson, mais diminue avec une augmentation du volume du repas et de la grosseur des particules de nourriture, et lorsque le poisson est gavé.

Nous avons déterminé les taux de consommation d'aliments et la chronologie de l'alimentation de l'abondante classe d'âge de 1966 du lac des Bois, en appliquant les résultats des essais de digestion en laboratoire à des échantillons de contenus stomacaux. Nous avons mis au point une méthode d'estimation qui tient compte des facteurs qui ont affecté la digestion au cours des essais de laboratoire, et cette méthode a servi aux calculs pour la population sur le terrain. La consommation est en moyenne de 1% du poids corporel en juin, 2% en juillet et 3% en août et septembre. Les températures moyennes sont semblables en juin et en septembre. Une plus grande consommation en septembre est le résultat d'une plus grande disponibilité de nourriture. Les poissons se nourrissent le plus la nuit et tôt le matin, à tous les mois sauf juin, alors qu'il se nourrissent de façon continue. Nous décrivons l'efficacité de conversion de la classe d'âge de 1966 à partir d'estimés de croissance et de taux de conversion durant les mois de juin à septembre inclusivement et arrivons à un chiffre d'environ 20% pour chaque mois.

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KNOWLEDGE of food consumption in fish populations is needed to interpret the influence of a variety of factors on fish production (Warren et al. 1964; Windell 1966; Brocksen et al. 1968; and Brett et al. 1969). Laboratory studies on digestion, metabolism, and food conversion efficiency have provided the basis for most estimates; techniques were reviewed by Davis and Warren (1968).

Measurement of gastric digestion rate provides a direct approach for estimation of food consumption rates (Kitchell and Windell 1968). Previous attempts at using the approach, however, have been based on limited data often obtained by force feeding or from fish recovering from the stress of capture. Estimation procedures previously applied are applicable in few situations (Davis and Warren 1968).

In the present study detailed information on gastric digestion rate was obtained from laboratory experiments with walleye, *Stizostedion vitreum vitreum*, and sauger, *S. canadense*. Effects of meal size, food particle size, fish size, and temperature were analyzed. Species differences, population differences, and influence of laboratory methods were studied. A method of applying digestion data was developed, which gives accurate estimates of daily consumption rate for the average individual from a field population. The technique is suitable for general use and can be used to describe feeding chronology and consumption of individual prey species. Estimates of average daily consumption rate, daily consumption rates of major prey species, and feeding chronology of the 1966 year-class of Lake of the Woods, Minnesota, walleyes illustrate the method. Estimates of consumption rate were used with information on growth rate to estimate conversion efficiency.

LABORATORY DIGESTION STUDIES

Materials and Methods

Digestion studies were conducted from October 1969 to April 1970, in three pools 2.44 × 0.6 m with volumes of 2100 liters. Mechanical agitators held oxygen concentration near saturation in a flow-through system of temperature-controlled water. Flow rates ranged from 2–6 liters/min. Experiments were conducted at 14.5 and 20±1.0 C. Photoperiod was set to duplicate conditions at Lake of the Woods from June through September. Weekly adjustments were made during a 15–30 day acclimation period to alter the photoperiod to the simulated time of year. Light intensity averaged 1-lm/ft^2 at the surface of the tanks. Most walleye and all sauger used in the laboratory were taken from Lake of the Woods, located in the northeast section of Minnesota; it is the state's largest lake and covers approximately 122,000 ha. During 1969 and 1970 when field samples were collected, the 1966 year-class made up over 50% of the important walleye population of this lake. Walleye from Lake Elysian (956 ha) and Sandshore Lake (15 ha) in southeastern Minnesota were also used. Fish ranged in size from 178 to 381 mm fork-length. Densities never exceeded 27 and averaged 20 fish per tank. Fish were not separated by size or species.

Fish were fed ad libitum on fathead minnows (*Pimephales promelas*) at the experimental temperature for a minimum of 5 days prior to running digestion experiments. Experimental groups were fed 2 additional days on a restricted schedule during which food was made available for 30 min. Adoption of the restricted schedule was required to train fish to accept food over a short period. This training and fasting of experimental groups the day prior to running digestion experiments increased acceptance of experimental meals. In experiments at 20 C, fish were allowed to feed for 30 min on fathead minnows each weighing 0.8 g. In experiments at 14.5 C, fathead minnows weighing 1.1–1.9 g or 3.1–5.0 g were fed.

In 2 of 25 experiments at 14.5 C, the walleye and sauger were anesthetized and force-fed 1.1–1.9-g minnows. Minnows used at 14.5 C were weighed to 0.1 g and marked with a colored thread sewn below the dorsal fin. Reference to the markers in the undigested remains allowed determination of original weight to 0.1 g and precise calculation of state of digestion.

Food remains were removed by pumping stomachs of anesthetized fish (M.S. 222 80–137 ppm). Glass tubes 11.5 and 15 mm in diameter, fired and tapered at the oral end, were used to remove food remains. Each tube was fitted with an inner 4-mm tube through which flushing water was forced. Use of fired glass tubes prevented damage to the stomach lining and allowed visual observation for completeness of pumping. Fish were returned to the tank and fed for 4 days followed by 2 days on the restricted schedule, before being included in additional experiments. State of digestion was determined from the live weight and weight of undigested remains after 14 days preservation in 10% formalin.

Results and Conclusions

SPECIES AND POPULATION EFFECTS

Voluntary feeding experiments with 1.1–1.9-g fathead minnows included observations on both walleye and sauger under similar experimental conditions and did not show a species difference. Experiments with both species included 84 observations on walleye and 21 on sauger, with 14 of those on sauger being made in experiments of 4-hr duration. Single degree of freedom orthogonal comparisons, used to test means from 4-hr experiments and control variability associated with meal size, showed the species effect was insignificant ($F_{1,32}$ 0.01, $P > 0.1$). Means from experiments of 8- and 12-hr duration did not vary more than 2%.

Comparison of results with walleye from three lakes showed population differences do not influence digestion rate. Means from eight duplicated experiments based on 99 compatible observations with reference to fish size, time, temperature, and meal size, showed no significant differences between populations (t-test, $P>0.1$). Means did not vary by more than 6.5%. On the basis of these findings, species and population designations have been deleted in the analyses which follow. Gastric digestion rates for sauger from Lake of the Woods and walleye from Sandshore Lake and Lake Elysian were considered suitable for estimation of food consumption in Lake of the Woods walleye. The tests suggest that broad application of digestion data in estimating consumption rates should be generally practicable.

EVALUATION OF EXPERIMENTAL PROCEDURES

Repeated use of experimental animals — Individual fish provided from 2 to 10 observations on gastric digestion as a result of the experimental methods. It is possible that repeated handling biased results. However, lack of stress and effect was indicated by two facts: growth of fish in the laboratory continued during the experimental work; and mean gastric digestion rates from five replicated experiments were not significantly different (t-test, $P>0.1$) irrespective of the number of times fish were handled.

Force feeding — Force-feeding experiments were conducted to evaluate the system used to mark original weight of food and to allow comparison with voluntary feeding studies. Evaluation of the technique was desirable since digestion data from force feeding are available for walleye (Hofmann 1969) and zander, *Lucioperca lucioperca*, (Molnar et al. 1967). Mean percentage digestion of force-fed meals from 1.1–1.9 g were 18.2% for 20 observations at 4 hr, and 32.4% for 20 observations at 8 hr; means for voluntary feeding were 36.0% for 30 observations at 4 hr, and 60.1% for seven observations at 8 hr. Comparison by t-tests showed force feeding does bias results ($P<0.001$) as suggested by Windell (1966). Data obtained by force feeding were considered inappropriate for estimating food consumption rates of Lake of the Woods walleye.

Influence of a substitute food source — Fathead minnows were used in laboratory studies since natural foods were not available during the experimental period. The principal foods of walleye in Lake of the Woods are yellow perch, *Perca flavescens*, cisco, *Coregonus artedii*, trout-perch, *Percopsis omiscomaycus*, and the mayfly, *Hexagenia limbata*, (Swenson 1972). Although substitution of fatheads for these foods could bias results, an in vitro experiment showed digestion of fatheads to be similar to digestion of perch, the most important forage species. Fatheads and perch of the same size were digested for 8 hr in a solution of 1-ppt, 1:10,000 pepsin at pH 1.0 and 50 C. Mean digestion was 84.2% for fatheads and 82.8% for perch. Differences were not significant (t-tests, $P>0.1$). A conclusion that the substitute food source did not influence the results is supported by Windell (1966), who reported digestion in bluegills, *Lepomis macrochirus*, is similar for a large variety of natural foods.

Form of digestion relations — First and second degree polynomial regressions were fitted to data from voluntary feeding experiments grouped according to temperature, food particle size, meal size, and duration (Table 1). The analysis showed relations between percentage digestion and time were linear. Digestion rates have generally been shown to decrease during late stages (Windell 1966; Magnuson 1969; Tyler 1970), not considered in this study because they would prevent determination

TABLE 1. Mean percentage digestion of three sizes of minnows by walleye after voluntary feeding. Number of observations is in parentheses.

Food size, temp., and duration (*hr*)	Meal size (*mg food/g fish*)		
	0.1–10	10–20	20+
0.8 g (20 C)			
4	50.4 (7)	47.1 (3)	32.2 (6)
8	88.2 (8)	74.2 (4)	62.2 (10)
12	96.9 (4)	95.8 (8)	90.0 (16)
1.1–1.9 g (14.5 C)			
4	36.0 (13)	32.9 (15)	28.0 (9)
8	60.1 (7)	54.9 (12)	44.2 (13)
12	84.3 (7)	75.0 (13)	60.8 (6)
16	97.3 (1)	96.0 (1)	77.8 (8)
3.1–5.0 g (14.5 C)			
4	8.5 (2)	13.3 (5)	12.0 (14)
8	46.2 (1)	29.8 (7)	27.9 (12)
12	–	58.5 (1)	40.0 (15)
16	–	–	67.2 (9)
20	87.3 (4)	–	84.8 (15)
24	96.1 (2)	91.2 (1)	94.4 (12)

of meal size from undigested remains. Inclusion of late stages would make multiple fish experiments infeasible and reduce the number of observations. Futher, as will be illustrated, the procedure developed to estimate consumption and feeding periodicity does not require information beyond the point of 90% digestion.

Influence of meal size — The experimental meal, expressed as milligrams/food consumed per gram of body weight (mg/g), was considered the second independent variable in relations of percentage digestion, time, and meal size. Slopes asssociated with meal size were negative, highly significant, and indicated a retarding effect of increased meal size on the state of digestion reached at any point in time (Table 2). Regression coefficients obtained from relations between percentage digestion and time, data subdivided according to meal size (Table 1), were compared to determine whether influence of meal size was time-dependent. No significant differences were found (*t*-tests, $P > 0.1$). These results agree with those of Tyler (1970).

Effect of meal size was also demonstrated by relation of digestion rate, expressed as grams digested per hour, to grams of food consumed (Table 2). Plotted data showed relations to be rectilinear. Slopes of regression lines were positive and highly significant. Therefore, although increased meal size significantly reduced the state of digestion reached at a point in time, it increased the amount of food being processed by the digestive system during a given period.

TABLE 2. Regression equations describing relations between percentage digestion (Y), time (X), and meal size (mg/g; X_1), and between grams of food digested per hour (Y_1) and meal size (grams; X_2). All coefficients are significant with $P = 0.001$.

Calculated relations	Variability associated with regression (r^2)
0.8-g minnows (20 C)	
$Y = 21.045 + X\,6.132$	.72
$Y = 28.571 + X\,6.553 + X_1\,-0.493$	.82
$Y_1 = 0.464 + X_2\,0.073$	.88
1.1–1.9-g minnows (14.5 C)	
$Y = 15.608 + X\,4.530$	.75
$Y = 21.469 + X\,4.797 + X_1\,-0.419$	.82
$Y_1 = 0.053 + X_2\,0.052$	.84
3.1–5.0-g minnows (14.5 C)	
$Y = -5.579 + X\,4.309$	.93
$Y = 0.279 + X\,4.321 + X_1\,-0.205$	.94
$Y_1 = 0.078 + X_2\,0.020$	.61

Influence of food particle size — Influence of differences in physical form of foods is shown by difference in slopes of regressions obtained from experiments involving 1.1–1.9-g and 3.1–5.0-g minnows (Table 2). The regression coefficients and partial regression coefficients describing the slopes of lines relating grams digested per hour to food consumed and percentage digestion to time, are significantly smaller for 3.1–5.0-g minnows ($P < 0.01$). It is assumed that increased surface area and/or decreased scalation associated with the smaller minnows enhances rate of gastric digestion.

Influence of fish size — An influence of size of fish ingesting food, on gastric digestion rate, is assumed by the use of an expression of meal size in terms of body weight. Previous work fails to clarify the effect of fish size on digestion (Hunt 1960; Windell 1966; Tyler 1970). Pairing observations on fish of different size, which consumed similar meals in experiments of the same duration, showed that larger fish could digest a meal (grams consumed) faster. Pairing of observations was restricted to fish which varied in size by more than 50-mm fork-length but which consumed meals of the same size to within 0.5 g or 5 mg/g of body weight; 42 paired observations were available for each test. Percentage digestion was greater for larger fish at any time with all sizes of food (Sign test, $P < 0.05$). With meal size expressed in milligrams consumed per gram of body weight (mg/g), percentage values were not influenced by fish size (Sign test, $P > 0.1$). Therefore, an expression of meal size in terms of body weight is appropriate and accounts for variability associated with fish size.

Precision of experimental work — The procedure used to estimate food consumption in wild stock required determination of the hours of digestion of food found in stomach samples from relations of percentage digestion, time, and meal size. To determine the precision with which digestion time could be predicted, confidence belts were established on percentage digestion and used to determine confidence intervals on hours of digestion, the independent variables in the regression relations (Snedecor and Cochran 1957). Figure 1 shows confidence belts on means and individual observations for data from experiments with 1.1–1.9-g minnows. The figure indicates the method used

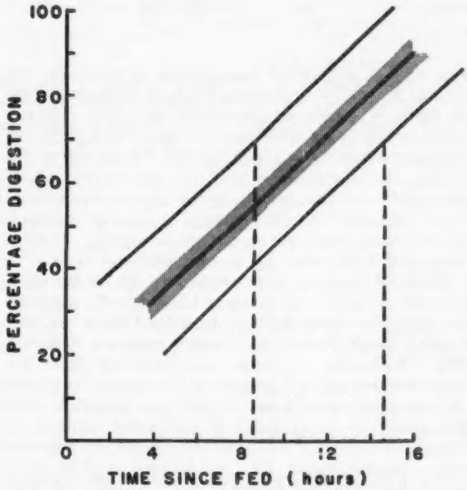

FIG. 1. Calculated relation between percentage digestion, time, and meal size in experiments with 1.1–1.9 minnows, 14.5 C. Shaded areas represent 95% confidence intervals on means. Outer lines are 90% confidence intervals on individual observations.

to obtain confidence intervals on digestion time and shows hours of digestion could be predicted from individual observations to within 6 hr ($P<0.1$). Confidence intervals for data on 0.8 g and 3.1–5.0-g minnows approximated 4.5 and 6.5 hr ($P<0.1$).

FIELD STUDIES

Materials and Methods

FIELD SAMPLING

Field samples were collected with an otter trawl (25-ft headrope, ¾-inch bar mesh and ¼-inch liner in the cod). Collections were made during day and night hours using a standard haul, which covered 2400 m^2 and filtered 3600 m^3 of water in 7 min of towing. Sampling was restricted to areas of sand and organic bottom. Catches provided the stomach samples used in describing consumption rates and feeding periodicity. Scale samples, length and weight measurements were taken for use in describing growth of the 1966 year-class.

EXTRAPOLATION OF LABORATORY RESULTS

To permit application of laboratory results to field data, temperatures and food sizes selected were representative of 75% of samples taken from Lake of the Woods. Samples collected at 17 C or containing food items approximating 0.3 and 2–3 g comprised a major portion of those for which data were not representative with respect to food particle size. When necessary relations between percentage digestion, time, and meal size were developed by extrapolation to fit particular temperature and food size condition. Extrapolation to obtain estimates of percentage digestion for durations from 0–4 hr were made by linear extension of calculated regression lines and by fitting lines by eye from values calculated for 4 hr to the XY intercept. Extrapolations to derive time of complete stomach evacuation were made by linear extension of calculated regression lines. Only extrapolations from 4 hr to the XY intercept were used in determining feeding rates and diel feeding periodicity (Fig. 2). Linear extrapolations of calculated regression lines were used to extrapolate to food sizes and temperatures not included in experimental work.

Extrapolations on food particle size and temperature were based on assumptions that faster digestion of smaller minnows in 14.5 C experiments resulted from the greater surface area (per unit weight), and that effects of differences in minnow size were proportional.

Proportionality was used in extrapolating for various food sizes. A surface–weight relation was used to predict surface area for various food sizes, and was obtained by measuring surface area of 52 minnows (0.15–4.50 g) and plotting surface area per gram on weight (Fig. 3).

Relations between percentage digestion, time, and meal size for a particular size food item at 14.5 C were obtained by using proportions. One ratio consisted of the difference in surface area/g between the two sizes of foods used in laboratory experiments at 14.5 C and the differences in the time at which 0 or 100% digestion was reached. The second ratio was the difference in surface area/g between laboratory food size and field food size. Solution gave estimates of change in time at which 0 or 100% digestion was attained as a result of

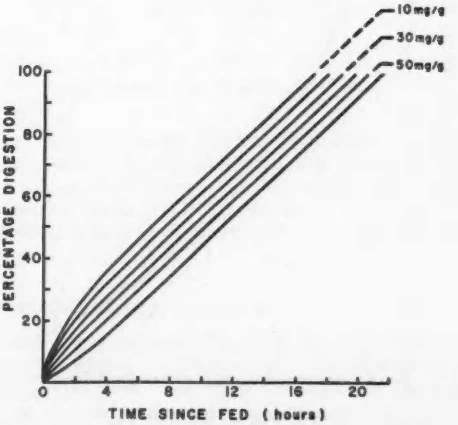

FIG. 2. Relation between percentage digestion, time, and meal size in experiments with 1.1–1.9 minnows, 14.5 C. The relation is described with meal size held at 10, 20, 30, 40, 50, and 60 mg/g.

change in food particle size. Correcting for this difference gave two points between which lines could be drawn to derive relations similar to Fig. 2.

Comparison of the extrapolated relation obtained for 0.8 g food at 14.5 C with that from laboratory data at 20 C allowed description of temperature effect. Determined in this manner, 5.5 C change in temperature resulted in a 15–20% change in time of 0 and 100% digestion, depending on size of the meal consumed. These values were applied to time of 0 and 100% digestion derived for various food sizes at 14.5 C, to extrapolate for a particular food size at 20 C. For 17.3 C, half the temperature effect was applied in correcting time of 0 and 100% digestion.

Estimation Technique

The method used to estimate food consumption is summarized by the equation:

$$C = \Sigma_t \, \Sigma_s \, \frac{(\Sigma_f \ SC)}{F}$$

Where C = daily food consumption in grams for the average fish; SC = undigested weight of stomach content for foods of a given size, not more than 90% digested, consumed during a time period; Σ_f = summation of corrected weight of stomach content for all fish in the sample, having consumed food of a size, during a time period; F = number of fish in the sample which could have contained food of a size, in a state of digestion not exceeding 90%, during a time period; Σ_s = summation of food sizes; Σ_t = summation of time.

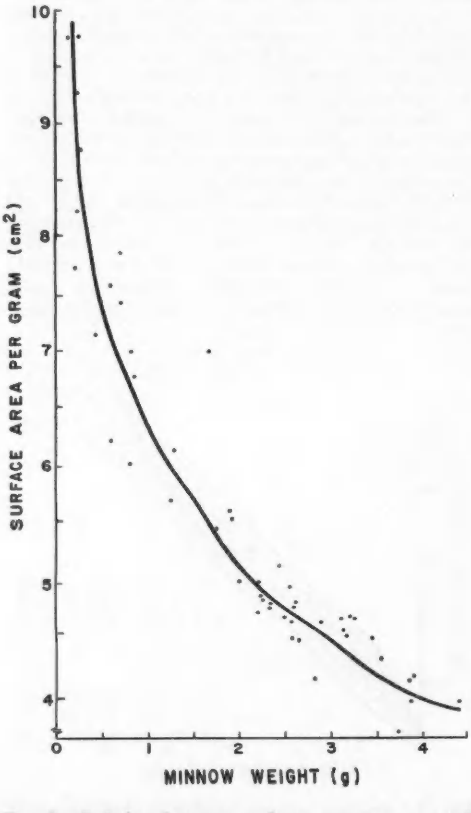

FIG. 3. Relation between surface area per gram of body weight and weight derived empirically from measurements on 52 fathead minnows.

Weight of stomach content was corrected for digestion, and state of digestion determined. Correction for digestion was made by measuring length of food items and calculating weight from length–weight relations (Swenson 1972). Percentage digestion was estimated from the corrected and digested weights. When length could not be measured accurately, percentage digestion was determined by comparison of undigested remains to displays of minnows of similar size digested to a known degree (approximately 10% gradations) in laboratory experiments. Original weight of the food item was then estimated from weight after digestion and estimated state of digestion.

In the analysis, percentage digestion and corrected weight were calculated separately for all food items which fell into five size categories for which relations between percentage digestion, time, and meal size had been derived. Calculations were also made separately for foods of the same size which varied in state of digestion by more than 20%. Food items of the same size which did not vary in state of digestion by more than 20% were considered to be part of the same feeding. Estimation of percentage digestion and original weight were derived for these items as a group.

Weight of a feeding, corrected for digestion, was converted to milligrams and expressed in terms of body weight of the fish which consumed it. Hours of digestion were estimated by reading the percentage time scales (Fig. 2). To increase accuracy, portions of earlier feedings were added to subsequent feedings in correcting for meal size. Ingestion time was calculated as time of capture minus hours of digestion. The amount of food consumed by all individuals in a day's sample was tallied according to ingestion time by 2-hr periods. Separate tallies were made for each food size category. Summation of feedings of a given size item, consumed during a given time period, gave the total weight of food, of a given size, consumed during each period. This value is an estimate of Σ_f SC in the equation.

The divisor, F, is estimated by using relations between percentage digestion, time, and meal size to calculate the number of hours required to reach 90% digestion. The value of F is then estimated by tallying back from the time of capture that number of hours, for each fish, and summing over all fish for each time period. Separate estimates were made for each size food item.

Division of Σ_f SC by F results in an estimate of the amount consumed of each food size during each 2-hr period by an individual in the sample. Estimates

TABLE 3. Estimated average daily food consumption of walleyes in Lake of the Woods, Minn.

Month and year	No. of days	Mean no. of fish	Mean fish wt. (*g*)	Total consumption *mg/g* Mean	Total consumption *mg/g* Range	Consumption of prey species (*mg/g*) *Perca flavescens*	*Coregonus artedii*	*Percopsis omiscomaycus*	*Notropis* spp.	*Hexagenia limbata*
June										
1969	9	18	179	13.6	7.4–27.4	1.1	5.4	1.4	2.3	1.1
1970	2	39	259	8.2	6.2–10.4	0.0	0.4	1.5	0.0	6.4
July										
1969	2	50	187	15.2	12.6–17.8	9.8	0.0	0.4	0.4	4.4
1970	3	38	312	23.3	14.0–33.7	12.3	0.2	0.1	2.1	7.6
Aug.										
1969	1	47	221	31.0	– –	28.4	0.3	0.0	2.3	0.0
1970	2	34	384	26.5	12.1–40.9	25.6	0.0	0.0	0.4	0.0
Sept.										
1969	2	59	285	29.6	20.0–39.1	28.9	0.4	0.1	0.1	0.0
1970	6	39	422	30.5	16.6–42.6	29.3	0.6	0.2	0.4	0.0

of daily consumption in grams are obtained by summing food sizes and time periods. Description of consumption in terms of body weight was obtained by dividing by average weight of fish in a sample. Since feedings consisted of one species it was possible to follow the procedure and arrive at estimates for each item in the diet.

Feeding periodicity was described by determining the percentage of the total meal consumed during each 2-hr period. Percentages were summed over periods that occurred during night, early morning, midday, and late afternoon. Division by the hours in each grouping resulted in an estimate of the percentage of the total meal consumed per hour during each of the four major periods of a day.

Results

FOOD CONSUMPTION RATES

Estimates of average daily food consumption by individuals of the 1966 walleye year-class in Lake of the Woods were made for 27 days from 924 fish collected during June through September of 1969 and 1970. Total consumption and consumption of major prey species were estimated (Table 3).

Variability associated with daily estimates and means for different months was not apparent between means of a given month for the 2 years sampled. Means for different months increased from June to August, with September similar to August. Changes in total consumption appear to be directly associated with increased consumption of perch, which in northern lakes increase in availability from July through September.

DIEL FEEDING PERIODICITY

Diel feeding periodicity was calculated for 16 days (Table 4). Comparison of means by Duncan's New Multiple-Range Test showed feeding is rhythmic during July through September, when activity is significantly greater during night and early morning hours ($P<0.05$). Data for June suggest feeding activity is uniformly distributed during that month.

TABLE 4. Feeding periodicity of Lake of the Woods walleye as percentage of the daily meal consumed per hour.

Month	No. of days	Dark (*night*)	Low light (AM)	Low light (PM)	High light (*midday*)
Period		22:00–04:00	04:00–08:00	18:00–22:00	08:00–18:00
June	2	3.4	5.5	4.2	4.3
July	4	8.1	6.9	1.2	2.0
Aug.[a]	5	5.7	8.8	3.1	2.1
Period		20:00–06:00	06:00–10:00	16:00–20:00	10:00–16:00
Sept.	4	3.3	7.5	3.1	4.1

[a]Includes samples taken Sept. 1 and 2, 1970.

FOOD CONVERSION EFFICIENCY

Food conversion efficiency of the 1966 year-class was calculated for each month (June–September) from estimates of consumption and growth. Growth was described from 672 fish collected during 22 days from June 10 through September 27, 1969 and from 719 fish during 20 days from June 15 through September 18, 1970. Lines were fitted by polynomial regression to mean weight of members captured on a given day (Fig. 4). Efficiency estimates ranged from 16.9% for June, 1969 to 60.1% for June, 1970 (Table 5). The high estimate for June, 1970 resulted from insufficient sampling. Growth was described from samples collected on 4 consecutive days. Information on consumption was based on 2 days. Omitting June, 1970, the results suggest Lake of the Woods walleye, in their third and fourth year of life, convert 20% of their diet to biomass.

Discussion

VALIDATION OF THE RESULTS

The accuracy of any method of estimating food consumption in wild fish stocks rests ultimately upon an assumption that laboratory results are representative of field conditions. The digestion rate method is best suited to meeting this assumption. Since other methods are dependent on laboratory measurements of more complex physiological processes such as metabolism, growth, nitrogen assimilation, and efficiency of utilization, they require more assumptions for extrapolation to field conditions (Mann 1967). To insure that results were representative in the present study, all sizes of fish and sizes of meals encountered in the field were included in the laboratory work. Experimental work was extensive enough to predict the effects of significant factors and to make extrapolations, based on reasonable assumptions, to temperature and food sizes not considered in the laboratory. Fish used in experiments were acclimated and accepted meals voluntarily. Although our experiments were conducted during winter months and used to describe digestion during the summer, Windell and Norris (1969) found digestion during winter months is representative of summer months in fish acclimated to summer temperatures.

TABLE 5. Growth, food consumption, and food conversion efficiency for the 1966 walleye year-class.

Period	Period[a] duration (*days*)	Growth (*g*)	Consumption (*g*)	Conversion efficiency (%)
June 1969	20	8.2	48.6	16.9
June 1970	14	18.2	29.9	60.9
Mean[b]		12.3	40.9	30.1
July 1969	30	20.0	84.8	23.6
July 1970	30	51.1	217.5	23.5
Mean		35.6	151.2	23.5
Aug. 1969	30	37.7	205.5	18.3
Aug. 1970	30	67.3	290.0	23.2
Mean		52.5	247.8	21.2
Sept. 1969	26	51.0	218.0	23.4
Sept. 1970	17	42.7	221.0	19.3
Mean[b]		47.7	219.2	21.8

[a] Period duration is the number of days in the given month after the first samples were collected and prior to the last collections for the year.

[b] Means weighted according to the duration of sampling.

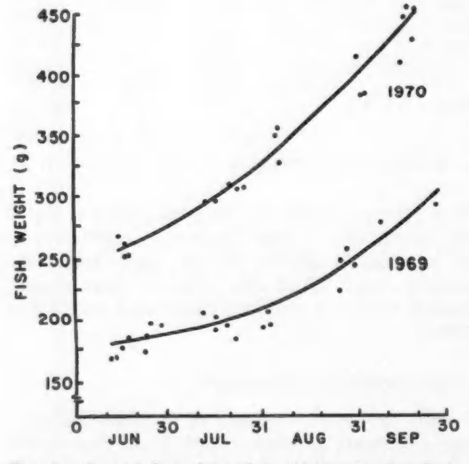

FIG. 4. Growth in weight of the 1966 year-class during 1969 and 1970. Growth during 1969 is described by the equation:

$$Y = 174.9 + 0.34276 + X^3\,0.00005,$$

and for 1970 by:

$$Y = 243.1 + X\,0.08972 + X^2\,0.00874.$$

Previous estimates of consumption based on the digestion method were considered inaccurate (Mann 1967). Inaccuracy arises in part from use of force feeding or recently captured fish in digestion studies (Seaburg and Moyle 1964; Ivanova 1968; Healey 1971). These procedures can be suspected of producing unreliable and variable results as indicated by our work and by Windell (1966). Inaccuracy of estimates is also due to use of methods which rely on the time required for complete stomach evacuation (Bajkov 1935; Ivanova 1968). Karpevitch and Bakoff (1937) have described digestion as a process comprised of an "effection phase" during which up to 90% of the food is digested rapidly and a "residual phase" in which hard parts are softened and passed slowly. The "residual phase" is variable in duration, being influenced by the extent of hard parts associated with food (Kionka and Windell 1972) and by ingestion of subsequent meals (Karpevitch and Bakoff 1937). The "effection phase" has not been shown to be influenced by either factor in fish with distinct stomachs (Karpevitch and Bakoff 1937). By eliminating the need for information on the "residual phase," the technique used in the present study removes variability associated with the digestive process and increases accuracy of results. By making estimates of consumption for all periods of the day, the procedure provides a means of estimating feeding periodicity and increases accuracy by eliminating possible bias associated with periodic feeding. Procedures which do not describe feeding rate for all periods of a day result in bias if feeding is periodic (Darnell and Meierotto 1962).

Estimates of consumption and food conversion of Lake of the Woods walleye were approximately equal to estimates derived from laboratory data on large-mouth bass, *Micropterus salmoides*, and *Megalops cyprinoides* of similar size (Markus 1932; Pandian 1967), but were higher than those derived by Hofmann (1969) for Lake Oneida walleye held in pools. However, Hofmann found growth was slower than in the lake and suggests food consumption was inhibited by confinement. Night feeding of walleye during July through September is confirmed by studies on walleye activity in Lake of the Woods, Minnesota, and Clear Lake, Iowa. From change in gillnet catches, Carlander and Cleary (1948) demonstrated that walleye activity was greatest in the two lakes during periods of darkness. Continuous feeding during June, as suggested by our results, seems logical in view of what we know about food abundance in northern lakes during this month. Greater fishing success during June further confirms the accuracy of the estimates.

APPLICATION OF THE METHOD

The digestion rate method is the only approach which allows description of consumption for a given day. Other methods require measurement of growth in field populations and, therefore, can provide only average estimates based on the period when growth was measured. Such estimates have limited application in determining the effects of factors which change over a short period. Effects of wing, air pressure, or short-term change in water quality on feeding activity cannot be evaluated from estimates based on growth of field populations. Our estimating technique gives accurate estimates of consumption for a given day, estimates of consumption of individual prey species, and descriptions of changes in feeding activity within a given day. Used in conjunction with information on food availability, the method permits assessment of the influences of food abundance on consumption, time of feeding, and efficiency of food conversion. Evaluation of the effects of predation on prey species is also possible. In view of the foregoing considerations it is beleived that a useful tool has been developed for a variety of ecological studies.

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Proecdysis, Setal Development, and Molt Prediction in the American Lobster (*Homarus americanus*)

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Aiken, D. E. 1973. Proecdysis, setal development, and molt prediction in the American lobster (*Homarus americanus*). J. Fish. Res. Board Can. 30: 1337–1344.

Setal development and proecdysial cuticular changes can be observed in the pleopods of the American lobster (*Homarus americanus*) from earliest D_0 through stage D_3, and with pleopod staging criteria it is possible to follow proecdysis from beginning to end. A technique is described for recognition of all stages and substages of proecdysis, for evaluating effects of various treatments on proecdysis, and for predicting time of ecdysis where holding temperature is known. Histological comparisons between the pleopods and the general integument suggest a universal criterion for stage D_2, and a need for adjustment in some accepted molt stage criteria. Development plateaus occur in stage D_0 instead of C_4 in this species, and this suggests that the concept of stage C anecdysis may be incorrect.

Aiken, D. E. 1973. Proecdysis, setal development, and molt prediction in the American lobster (*Homarus americanus*). J. Fish. Res. Board Can. 30: 1337–1344.

On peut observer le développement des setae et les changements cuticulaires de la proecdysie sur les pléopodes d'*Homarus* à partir du tout début de D_0 jusqu'au stade D_3 et, par des critères définissant les stades des pléopodes, il est possible de suivre la proecdysie du début à la fin. L'auteur décrit une technique permettant d'identifier tous les stades et sous-stades de la proecdysie, d'évaluer les effets de divers traitements sur la proecdysie et de prédire l'époque de l'ecdysie lorsque la température à laquelle les homards sont maintenus est connue. Une comparaison histologique entre les pléopodes et le tégument général suggère un critère universel pour le stade D_2 et un besoin de reviser certains critères acceptés des stades de la mue. Il se produit des plateaux dans le développement au stade D_0 plutôt qu'au stade C_4 chez cette espèce, ce qui donne à croire que le concept d'anecdysie au stade C est peut-être erroné.

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Proecdysis (premolt, or stage D) is a period of biochemical and morphological change in preparation for the next ecdysis, and some of the morphological changes have been used as criteria for the various substages of proecdysis since the pioneer work of Drach (1939)[1]. External changes are easily identified in some stages of the molt cycle, but most of the events associated with early proecdysis occur internally. Two notable external features of this stage are limb bud regeneration and decalcification, but the former is not obligatory and is therefore unreliable under certain conditions (Sochasky et al. 1973), and the latter occurs too late to be of any real help in proecdysial staging.

A simple, accurate staging method for proecdysis is essential to the study of lobster molt physiology, and several methods have been described. However, Hepper's method (1965) is inconvenient because it requires histological sections and is not correlated with standard molt stages, the color index of Barlow and Ridgeway (1969) is not reliable early in proecdysis, and the criteria described by Donahue (1954) proved to be inaccurate. Recently Rao et al. (1973) described a technique for staging larval lobsters by setogenic changes in the transparent telson and uropods, but these appendages are opaque and thus unsuitable for use in staging juvenile and adult American lobster (*Homarus americanus*).

For the past 5 years pleopod setogenesis has been used for staging juvenile and adult lobsters at this laboratory, and a method has been developed

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[1] Drach (1944) and many others have modified the original scheme so that it is now applicable to a variety of crustaceans. For example see Hiatt 1948, Charniaux-Legrand 1952, Donahue 1954, Travis 1955, Knowles and Carlisle 1956, Carlisle 1960, Charniaux-Cotton 1957, Passano 1960, Scheer 1960, Crisp 1960, Kurup 1964, Hepper 1965, Drach and Tchernigovtzeff 1967, Nagabhushanam and Ranga Rao 1967, Stevenson et al. 1968, Barlow and Ridgeway 1969.

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for recognizing all substages of proecdysis and for predicting time of ecdysis where holding temperature is known. This paper describes the application of this method and discusses some of the problems encountered with accepted molt stage criteria.

Proecdysis

Stage D is generally divided into five substages, based on distinct physiological events: retraction of the epidermis (D_0); formation of new setae (D_1); synthesis of the pre-exuvial cuticle (D_2); decalcification of strategic regions of the old cuticle (D_3); and water absorption and splitting of the carapace along decalcified sutures (D_4).

THE INTERMOLT–PREMOLT TRANSITION

In the traditional concept of the crustacean molt cycle stage C_4 — "intermolt" — is regarded as a period of relative physiological stability. This stability is thought to continue indefinitely in the absence of molting hormone, or as long as the molting hormone is suppressed by molt inhibiting hormone, and this has given rise to the concept of anecdysis in C_4 (Carlisle and Dohrn 1953; Knowles and Carlisle 1956). The transition from the stability of stage C_4 to the extensive physiological change of proecdysis supposedly occurs abruptly when the molting glands are released from the inhibitory influence of the molt inhibiting hormone. Thus the stage C to stage D transition is depicted as a dramatic event when the physiological serenity of intermolt gives way to the biochemical and morphological changes characteristic of proecdysis.

Actually the evidence suggests that the C–D transition in *Homarus* is more gradual, with the characteristics of C_4 blending with those of D_0 over a considerable period of time. The really dramatic changes occur not in the C–D transition, but in the D_0–D_1 transition, and D_0 appears to be a period of flux when the animal is not clearly in either C or D. Apolysis, limb bud growth, and gastrolith development are accepted proecdysial events that originate in D_0, but these seem to start and proceed independently of one another (Stevenson et al. 1968). Apolysis is described as the first morphological indication of proecdysis (Drach and Tchernigovtzeff 1967), but apolysis does not begin uniformly throughout the body, and there is variation even in such similar structures as the exopodite and endopodite of the same pleopod!

Anecdysis (Carlisle and Dohrn 1953) and terminal anecdysis (the C_4T of Hiatt 1948) are terms that refer to a temporary or permanent pause between one molt cycle and the next, and this developmental pause has been assigned to stage C_4 (see Knowles and Carlisle 1956). In other words, the animal terminates one cycle at C_4, and fails to enter proecdysis. In *Homarus* a developmental plateau analogous to anecdysis is quite common but it occurs in early to middle D_0, not in C_4. Apolysis can be clearly demonstrated in the pleopods of lobsters in these developmental plateaus and this condition is defined as stage D_0 (Drach and Tchernigovtzeff 1967). Lobsters will pass through C_4 and into D_0 without pause during the cold winter months but development will not proceed beyond the initial stages of epidermal retraction until the water warms in the spring. Even then both sexes will occasionally maintain this plateau well into or even through the following summer. In his 1948 description of C_4T, Hiatt stated that the membranous layer of the cuticle, which is present in C_4, fuses with the principal layer and disappears in C_4T. This is typical of the fate of the membranous layer in D_0. Significantly, Hiatt's staging system did not include D_0; it went directly from C_4 to D_1. Permanent developmental plateaus that occurred between stages C_4 and D_1 were called C_4T by Hiatt, and there is little question that this C_4T is synonymous with D_0 as we know it today. This is probably also true for the stage C anecdysis of Carlisle and Dohrn (1953).

There is no question that D_0 is a valid stage because its characteristics can be clearly defined. However, there is some question whether this stage should be considered proecdysis in the sense of stages D_1 through D_4. In lobsters there is no obvious pause between stage A and D_0, or between D_1 and ecdysis. Whenever a plateau occurs in *Homarus* it is at that stage we define as D_0 — after onset of apolysis but before epidermal retraction has reached maximum. In this sense D_0 is more of a "resting" state than is C_4. In this context it is interesting that Drach originally (1939) included the phenomena of D_0 in stage C_4, and started proecdysis with stage D_1. Not until 18 years later did D_0 displace D_1 as the first stage in proecdysis (Charniaux-Cotton 1957). For the purposes of this paper and the staging criteria described herein, D_0 is considered to start with apolysis and to be a special stage of proecdysis — a broad transitional phase between obvious intermolt and obvious premolt, and a period when the lobster may simultaneously display the characteristics of both stages. Because of this broad overlap a lobster is considered to be in stage D_0 when apolysis is evident in at least one pleopod, irrespective of the number of pleopods that fail to show any suggestion of apolysis.

STAGE D_0

Separation of epidermis and cuticle between the bases of the setae is the first morphologically discernible indication of D_0 (Drach and Tchernigovtzeff 1967). My histological sections (Bouins fixation, Mallory trichrome) show that this separation (apolysis) occurs earlier in pleopod tips than in the carapace, abdomen, or telson. However, before separation occurs in the pleopod tip an amber-colored zone forms and there is evidence of reorganization (note the chromatophore displacement in Fig. 4C). A similar "amber colored" zone was noted in the uropods of *Petrolisthes* (Anomura) by Kurup (1964), who described it as "...lined by a membrane apparently formed by the condensation of some kind of secretion discharged by the epidermal cells." This sounds like a D_0 phenomenon, but Kurup compared it with the "couche membraneuse" of C_4 *Cancer* described by Drach (1939)[2]. In *Homarus* this amber zone appeared to be associated with apolysis. To check this, I compared pleopod changes with gross morphology and histology of the gastrolith plate. Seventy-nine lobsters (randomly male and female; sizes 52–87-mm carapace length) were staged by pleopods and sacrificed for comparison with gastrolith development. Results are summarized in Table 1. None of those rated C_4 or earlier showed any gastrolith development, whereas 97% of those with stage 1.0 pleopods (amber zone) displayed some gastrolith development, and in 18% of these there was some calcification. This is supported by Rao et al. (1972), who reported that radiograms of crayfish gastroliths showed that calcification commences either with or shortly after the onset of epidermal retraction. Thus the amber zone at the tip of the pleopod was associated with some degree of gastrolith development 97% of the time, and for this reason I consider it to be the first morphological indication of D_0 in *Homarus* pleopods.

Two other events associated with D_0 — limb regeneration and gastrolith formation — continue throughout the stage. As indicated in Table 1, gastrolith calcification had commenced in 18% of lobsters rated as early D_0, but 100% incidence of calcification was not reached until late D_0. The same variation might be expected for limb bud regeneration (Stevenson et al. 1968; Stevenson and Henry 1971).

TABLE 1. Pleopod and molt stage compared with gastrolith development. Numbers in brackets indicate percent in which there was cellular growth on the gastrolith plate.

Pleopod stage[a]	Molt stage	Sample size	% with gastrolith calcification	Mean gastrolith factor[b]
	C_4	4	0(0)	0
1.0	D_0	34	18(97)	10
1.5	D_0	16	88(100)	39
2.0	D_0	1	100	58
2.5	D_0	4	100	174
3.0	D_1'	2	100	163
3.5	D_1''	–	–	–
4.0	D_1'''	8	100	297
4.5	D_2'	4	100	350
5.0	D_2''	2	100	432
5.5	D_3	4	100	468

[a] See Table 3 for description of pleopod stages.

[b] $\frac{\text{gastrolith (mg)}}{\text{carapace length (cm)}} \times 100.$

STAGES D_1 AND D_2

In *Homarus* I have assigned maximum setal invagination to D_1''' and obvious barbule development to D_2'. This contrasts with the criteria of Tchernigovtzeff (1965) and Drach and Tchernigovtzeff (1967), who place maximum setal invagination in D_1'' and obvious barbule development in D_1'''. However, Tchernigovtzeff (1965) admitted that one rarely finds obvious barbule development before the cuticular secretion of stage D_2 has become apparent on the epidermis between the setae. In their 1967 revision, Drach and Tchernigovtzeff changed "secretion cuticulaire" (epicuticle only?) to the more specific "couche préexuviale," a synonym for pigmented layer. In other words, they include obvious barbule development and epicuticle secretion in stage D_1''', but when the pigmented layer forms on the epidermis between the new setae the animal is in D_2.

At first this appears to agree with Drach's general statement that D_2 commences with secretion of the pigmented layer, but this is complicated by the fact that onset and rate of formation of the pigmented layer vary with anatomical location. Drach (1939) mentioned the carapace and the terminal segment of a walking leg in this connection, and in *Homarus* the formation of pigmented layer in the carapace usually coincides with epicuticle secretion in the pleopods. Thus if carapace pigmented layer is accepted as the standard for D_2 (see following section) then the formation of new epicuticle on the pleopod epidermis signals the onset of D_2. This is further supported by stained pleopod sections. Tchernigovtzeff (1965) said that stage D_1''' is a transitory stage when barbules are present but no cuticle is formed on the epidermis between the setae, and as can be seen from Table 2, this condition occurs in pleopod stage 4.0. These barbules do not become obvious in unstained pleopods until pleopod stage 4.5, but by then the epicuticle is present on the pleopod epidermis, the pigmented layer is being formed in the carapace integument, and the animal is properly in D_2'.

These same sections reveal that the pigmented layer is not secreted at a uniform rate even in a single pleopod. A typical section in D_2'' shows that although the pigmented layer is very thick on the epidermis between the bases of the setae, there is no sign of new pigmented layer on the epidermis in the central region of the pleopod. Formation of the pigmented layer in the central region

TABLE 2. Sequential development of setal barbules and new cuticle in *Homarus* pleopods.

Pleopod stage[a]	Barbules	Pleopod epicuticle[b]	Pleopod pigmented layer[b]	Molt stage
4.0	yes	no	no	D_1'''
4.5	yes	yes	no	D_2'
5.0	yes	yes	yes	D_2''

[a] See Table 3 for description of pleopod stages.

[b] On the epidermis between the bases of the new setae.

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[2] Scheer (1960) and Kamiguchi (1968) described the epidermis of *Palaemon* as being slightly separate from the cuticle in stage C_b (comparable to C_3–C_4; see Drach and Tchernigovtzeff 1967), but it is difficult to tell whether this is the same phenomenon.

coincides with progressive decalcification of the ecdysial sutures, and thus occurs in stage D_3. This final phase of pigmented layer formation produces the cuticular folds that are visible in a stage 5.5 pleopod (Fig. 2B, 3A, 4R), and which presumably contribute to increase in volume following ecdysis.

UNIVERSAL CRITERIA FOR D_2

In 1968, Stevenson et al. stated that "...precedent now demands that stage D_2 be defined as beginning when secretion of new epicuticle begins, even though it may be impossible to determine precisely when this occurs in the living animal." At approximately the same time, Drach and Tchernigovtzeff (1967) redescribed the criteria for D_2 in several ways, including formation of new pigmented layer in the carapace region, and appearance of new cuticle between the bases of developing setae. In a final table (p. 602) they give the criterion for D_2 as "...la couche préexuviale visible à la surface de l'épiderme banal entre les soies." The word "visible" connects stage D_2 to an apparent rather than an actual event and makes the D_2 criterion arbitrary. This is also true of their criterion for D_1''', where barbules must be "très apparentes" on the setae even though, as the authors admit in a footnote, these barbules are actually forming early in D_1'. Thus the criteria of Drach and Tchernigovtzeff associate two important proecdysial stages — D_1 and D_2 — with apparent rather than actual events, and thus make interspecific comparisons difficult.

Much of this difficulty could be eliminated if we follow the reasoning of Stevenson (1972) and select a standard anatomical location and event to characterize stage D_2. Any external change could then be used as an index of D_2 once it had been correlated with the standard. The basis for this has been established by Drach and Tchernigovtzeff (1967) who clearly state (p. 598) that stage D_2 is characterized by secretion of the pigmented layer, and suggest that the carapace is a good place to observe the formation of this layer. I suggest that we formalize this by defining stage D_2 as that point in proecdysis when there is histological evidence of new pigmented layer adjacent to the midline in the gastric region of the carapace (for "gastric region" see Stevenson et al. 1968). Any other event that coincides with this standard for a particular species can then be used as evidence of stage D_2. In post-larval *Homarus* the most convenient index of D_2 is found in the pleopods; in larval *Homarus* (Rao et al. 1973) and in *Orconectes* (Stevenson 1972) the telson and uropods apparently provide similar information.

Setal Development

In *Homarus*, each new seta invaginates into and develops within a cylindrical structure that I have tentatively termed a setal organ (Fig. 1, 2). Each of these so-called setal organs seems to be associated with a blood vessel (Fig. 2E), and frequently contains large numbers of blood cells (Fig. 2A, B). After epidermal retraction is completed a papilla develops around the base of each of the retracted setae (Fig. 1B, 2A) and this is followed by epidermal growth and invagination into the setal organ (Fig. 1C). Barbules are also developing on the setal shaft at this stage (they point distally whether formed on the proximal or distal portion of the setal shaft; Fig. 2D). The barbules and the setal shafts thicken as new epicuticle and pigmented layers are formed. In stage D_3 the fully formed setae are inverted within the setal organ (Fig. 2C) and the new integument undergoes rapid growth, forming folds that presumably allow for increase in volume following ecdysis (Fig. 2C, 3A). During ecdysis the new setae evert like the fingers of a glove (Fig. 3B–D).

The general details of early setal development are similar for a variety of crustaceans, but various authors have described the formation of the new setal shafts in different ways. Drach (1944) said that the distal portion of the shaft was secreted by a "faisceau nerveux axial" in shrimp; Kurup (1964) felt that the setae of the anomuran *Petrolisthes* developed long shafts by growing "both at

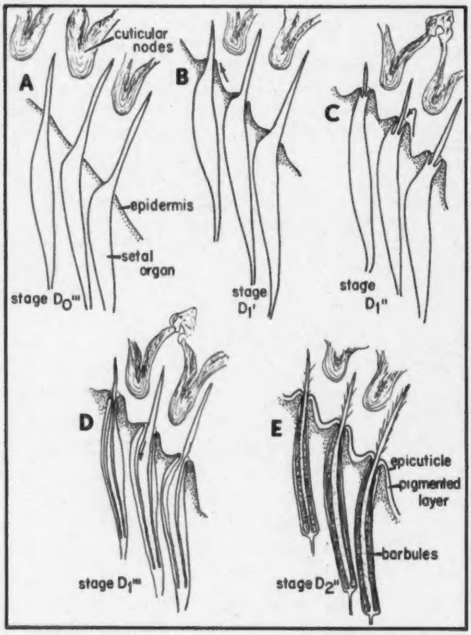

FIG. 1. Steps in the formation of new pleopod setae during proecdysis. A — maximum retraction of the epidermis. B, C, D — progressive invagination into the setal organ. E — completed setae inverted within the setal organ.

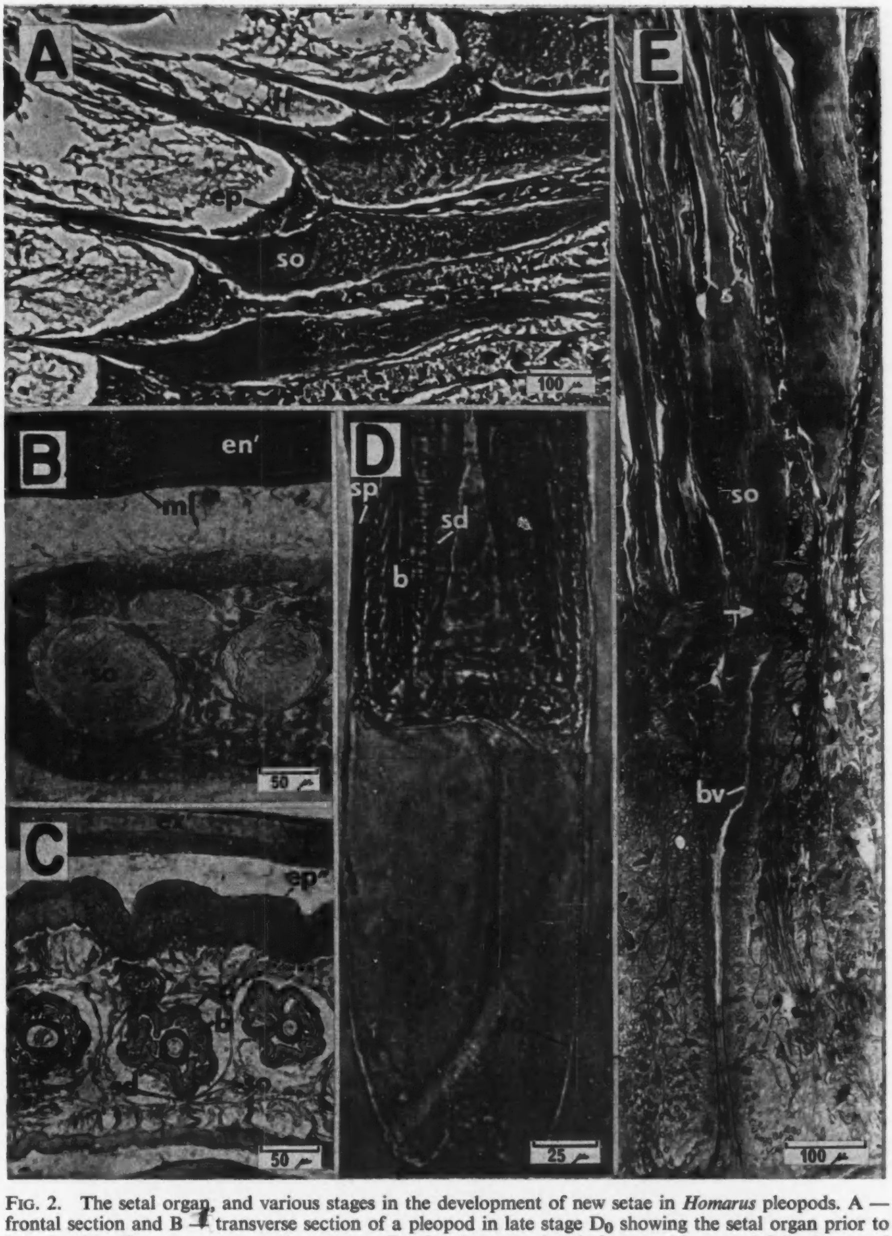

FIG. 2. The setal organ, and various stages in the development of new setae in *Homarus* pleopods. A — frontal section and B — transverse section of a pleopod in late stage D_0 showing the setal organ prior to invagination. C — transverse section at stage D_3 showing convoluted pigmented layer and fully developed new setae inverted within the setal organ. D — new seta and setal organ dissected from fresh pleopod in stage D_3. E — frontal section of a pleopod in stage D_2' showing the relation between blood vessels and setal organ (arrow indicates point of contact). Abbreviations: b, barbules; bv, blood vessel; en, calcified layer (endocuticle or principal layer); ep, epicuticle; ex, pigmented layer; ff, core of old seta; ml, membranous layer; s, invaginated portion of new seta; sd, distal part of new seta; so, setal organ; sp, proximal part of new seta. The old cuticle is designated by (′) and the new cuticle by (″) following the appropriate abbreviation.

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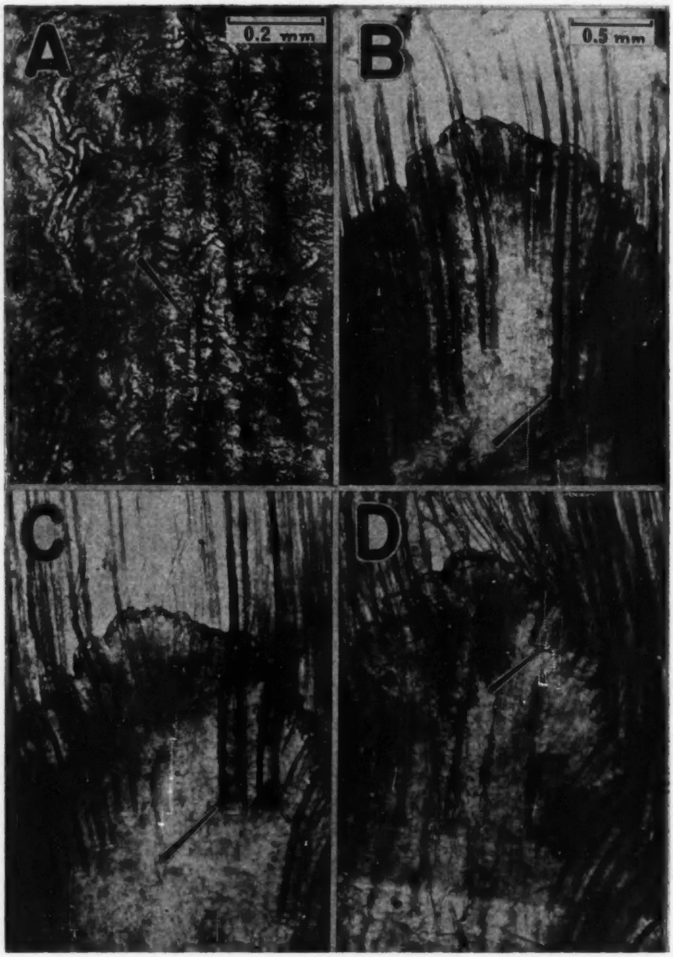

FIG. 3. A — cuticular folds that develop in the pre-exuvial cuticle during stages D_3–D_4, and presumably allow increase in volume following ecdysis. As the pleopod starts to withdraw from the exuviae (B) the invaginated setae progressively evert (C,D) like the fingers of a glove and assume their normal orientation.

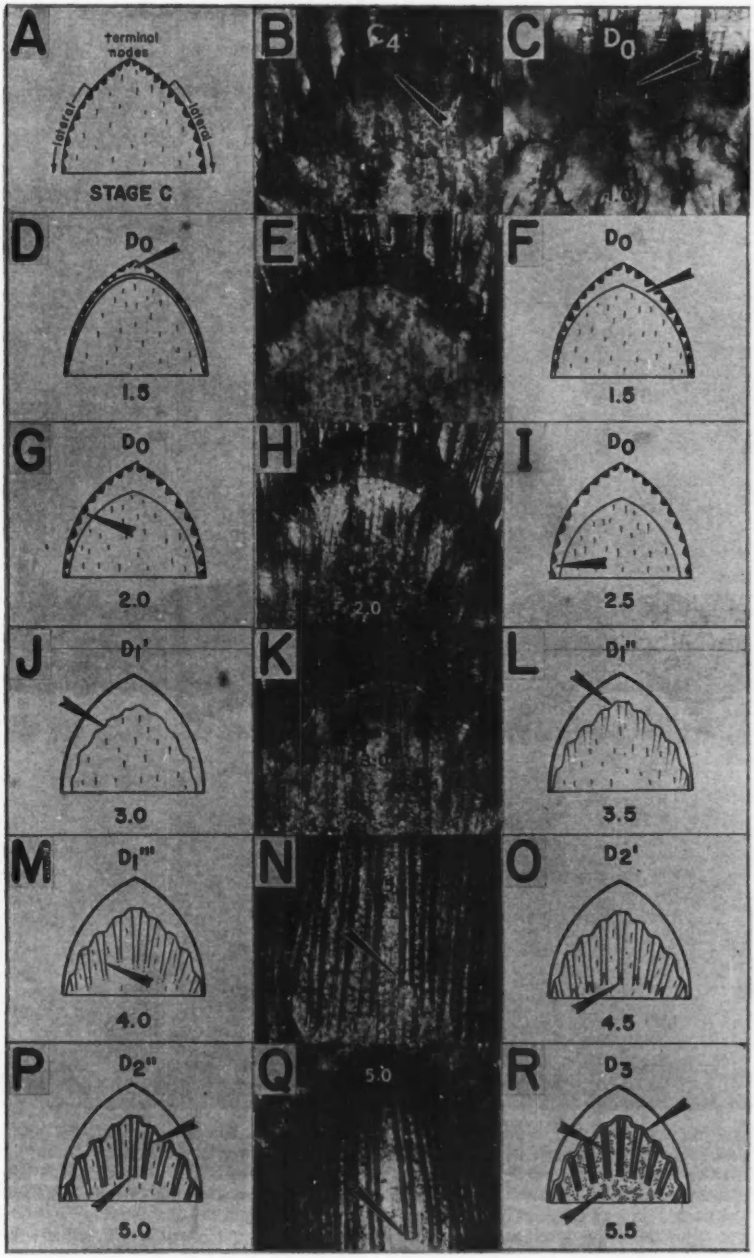
A
terminal nodes
lateral
lateral
STAGE C
B
C4
C
D0
1.0
D
D0
1.5
E
1.5
F
D0
1.5
G
D0
2.0
H
2.0
I
D0
2.5
J
D1'
3.0
K
3.0
L
D1''
3.5
M
D1'''
4.0
N
O
D2'
4.5
P
D2''
5.0
Q
5.0
R
D3
5.5

FIG. 4. Morphology of *Homarus* pleopods during intermolt (A,B) and proecdysis (C–R).

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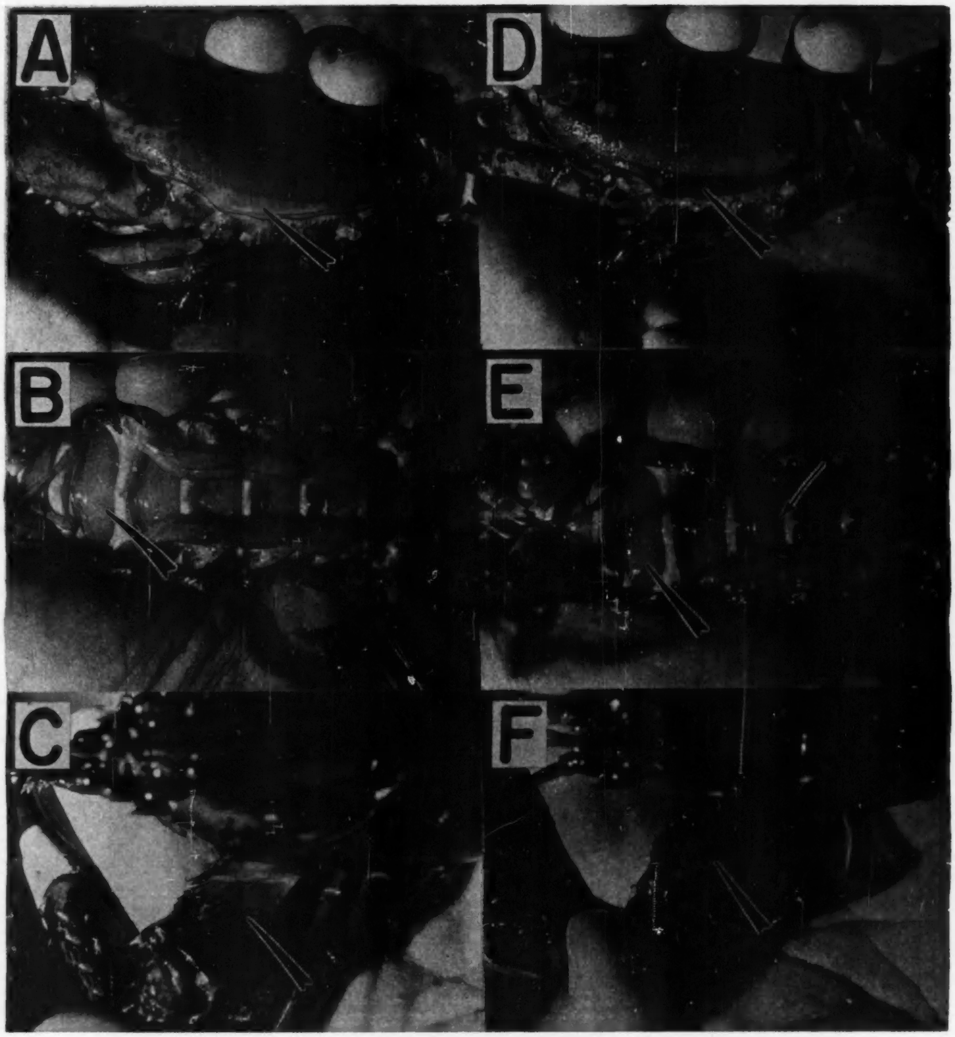

Fig. 6. Changes in the cuticle of *H. americanus* from intermolt (A–C) to late proecdysis (D–F). The lower margin of the carapace is firm and light colored during stage C (A) but becomes progressively darker during proecdysis (D), and turns soft within 3 days of ecdysis. Similar changes occur in the merus of the cheliped, which is firm and pale during stage C and most of proecdysis (C), but becomes dark blue about a week before ecdysis and very soft when the animal is within 2–3 days of ecdysis (F). The clear, white ventral abdomen of an intermolt lobster (B) becomes pink during proecdysis and often develops dark mottling (arrow in E) as much as 2 weeks before ecdysis.

their tips and at their bases," and Stevenson et al. (1968) described crayfish setal shaft development as the union of a tube within a tube.

Because of the morphological similarity between the latter stages of setogenesis in *Homarus* and published photographs and descriptions of this same event in other crustaceans it seems probable that *Homarus* is not unique in possessing a setal organ, and that setae develop in essentially similar fashion in other crustaceans as well. For example, fig. 8 and 9 of Kamiguchi (1968) quite clearly show this setal organ in the shrimp *Palaemon,* but it is identified simply as "invaginated part of new setae." Less clear but still indicative is the photograph of the branchial epipodite of the crab *Carcinus* (Tchernigovtzeff 1965, fig. 7). In the anomuran *Petrolisthes*, Kurup (1964) described the developing setae in their "respective crypts" and the fully formed setae in "setal sheaths that appear to have been derived from the epidermal invagination." Stevenson et al. (1968) describe a "cylindrical zone with lower cell density" extending inward from each seta in crayfish, and their diagrams correspond well with the same process in *Homarus*. All of this suggests that development from a "setal organ" is the normal process in Crustacea.

Molt Staging and Prediction

New setae are formed during the first half of proecdysis, and the different steps in their development have been used as an aid to molt cycle staging in the Anomura, Natantia, Brachyura, and Macrura.[3] Unfortunately, few species have a linear row of setae located on transparent appendages that are both abundant and accessible, and without this the method has limited value. In *Homarus*, a row of setae is found on the relatively large, abundant, and transparent pleopods, making repeated observations possible. In addition, progressive changes can be observed in these pleopods from earliest D_0 through the end of D_3, making this a more comprehensive index than that available in crayfish (Stevenson 1972) or larval lobsters (Rao et al. 1973).

PLEOPOD STAGING TECHNIQUE

An instrument could be designed to permit an unlimited number of in situ observations but the present technique, like that described by Tchernigovtzeff (1965), utilizes the severed tips of the pleopods. This limits the number of samples to a maximum of 16 per lobster. Fresh material must be used, as fixation can cause misleading epidermal retraction. The terminal one-third or one-quarter of a pleopod exopodite or endopodite is removed, placed concave (posterior) surface downward in a drop or two of sea water on a microscope slide, covered gently with a cover slip, and examined with transmitted light at approximately 40×. If setal shafts are not present in the central region of the pleopod (Fig. 4N, Q), concentrate on the distal tip of the pleopod. In a stage C lobster there is no sign of reorganization or epidermal retraction at the pleopod tip (Fig. 4A, B). In pleopod stage 1.0 (D_0) an amber zone appears at the tip (Fig. 4C) and this is followed by actual retraction of the epidermis from the thickened cuticular nodes that flank the setae. If this retraction is limited to the terminal nodes the pleopod is rated stage 1.5; if there is retraction from some of the lateral nodes as well it is pleopod stage 2.0. Pleopod stage 2.5 occurs when the epidermis is retracted from all terminal and lateral nodes, and the animal is in late D_0. The criteria for these and the other pleopod stages are summarized in Table 3, and illustrated in Fig. 4.

PREMOLT CURVES

An indication of rate of progression through proecdysis can be obtained by sampling the pleopod stage of an individual or group at regular intervals, plotting the stages against time, and fitting a curve by eye. These so-called "premolt curves" (Fig. 5) show relations between individual responses or different treatments. Premolt curves of individual lobsters are of three types. The Type 1 curve rises smoothly from onset of D_0 to ecdysis. This is the normal response to eyestalk ablation (Sochasky et al. 1973) and is also common when the water warms during the winter–spring transition. The other two types of curves contain D_0 development plateaus of varying length. The plateau may break within 4–6 weeks (Type 2) or continue for much longer (Type 3).

When individuals in D_0 plateau (Type 3 curve, Fig. 5) are repeatedly sampled over a period of several months, the plotted points often vary from 1.5 to 2.0 instead of falling on a straight plateau line. To determine whether this was due to variation between pleopods on the same animal, I examined all pleopods on 47 lobsters. No variation was found in lobsters in D_1' or later, but 18 of 31 lobsters in D_0 (pleopod stages 1.0–2.5) showed some variation. This was commonest in the C_4–D_0 transition and in pleopod stages 1.5–2.0. This probably accounts for the variation observed during D_0 plateau, but it also means that the occa-

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[3] Drach and Tchernigovtzeff 1967, Kamiguchi 1968, Kurup 1964, Schafer 1968, Scheer 1960, Stevenson 1972, Stevenson et al. 1968, Tchernigovtzeff 1965.

TABLE 3. Criteria for staging proecdysis from pleopods of *Homarus*.

Molt stage[a]	Pleopod stage	Description
C_4	0	Epidermis closely applied to cuticular nodes at tip of pleopod; no amber zone or epidermal retraction at pleopod tip (Fig. 4B).
D_0	1.0	First indication of apolysis — amber or double-bordered region forms at the pleopod tip. Chromatophores often show signs of reorganization but there is no epidermal retraction from the cuticle (Fig. 4C).
D_0	1.5	Epidermis retracting from terminal cuticular nodes; may have double-bordered appearance (Fig. 4D, E, F).
D_0	2.0	Epidermal line clearly formed and retracting from lateral cuticular nodes (Fig. 4G, H).
D_0	2.5	Maximum epidermal retraction — not touching any lateral cuticular nodes (Fig. 4I).
D_1'	3.0	Invagination papillae form at site of future setae; epidermis becomes scalloped (Fig. 4J, K).
D_1''	3.5	Invagination papillae clearly formed but shafts of new setae not well defined (Fig. 4L).
D_1'''	4.0	Shafts of developing setae visible but proximal ends not clearly defined (Fig. 4M). Shafts now invaginated to maximum length.
D_2'	4.5	Shafts visible full length but proximal ends are bifurcate instead of blunt (Fig. 4N, O). Barbules becoming visible on setal shafts.
D_2''	5.0	Shafts of developing setae thick, proximal ends blunt (Fig. 4P, Q).
D_3'	5.5	Shafts of setae very thick and dark, proximal ends blunt. Classify as D_3'' if folds or ripples are visible in cuticle on upper surface of pleopod (Fig. 4R).

[a] Modern version of system developed by Drach (1939).

sional D_0 lobster will be identified as C_4 if only one pleopod is examined. In experiments where recognition of the C_4–D_0 transition is important it would be advisable to examine several pleopods on any lobster initially rated as stage C_4.

Molt Prediction

Internal and external changes can be used to predict time of ecdysis in *Homarus*. Internal changes, exemplified by pleopod morphology, are more reliable and permit fairly accurate estimates spanning a month or more. External criteria are more convenient to use but are less accurate unless the animal is within a few days of ecdysis. Since the two methods complement each other they are both described here.

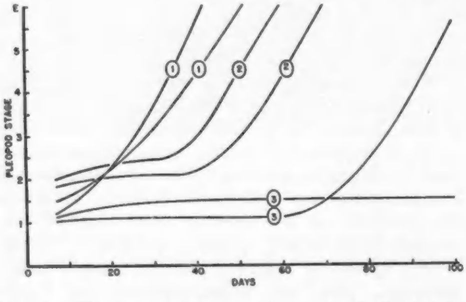

FIG. 5. Three types of premolt curves (indicated by appropriate numbers) produced by six lobsters held at a constant 19 C. Pleopod samples at 14-day intervals.

PLEOPOD STAGES

More than 700 pleopod samples were obtained from 120 lobsters, 55–75-mm carapace length, equally divided among three temperatures (10, 15,

TABLE 4. Days to ecdysis for a given pleopod stage and temperature. Values encompass ± one standard error of the mean, expressed in whole days. Development plateaus in stage D_0 affect the reliability of prediction for stages below the broken line (see text for discussion).

Pleopod stage	Temperature 10 C (*50 F*)	15 C (*59 F*)	19 C (*66 F*)
5.5	4	3	2
5.0	6–8	6	5
4.5	13	9–11	8
4.0	20–22	15–17	11–13
3.5	27–33	20–22	13–17
3.0	36–40	26–28	18–20
2.5	48–52	39–41	28–32
2.0	71–79	54–56	37–43
1.5	86–94	68–72	50–60

19 C) starting in late winter of two successive years. Additional observations were made on larger lobsters in less systematic fashion. Time to ecdysis from each stage was recorded and these data, summarized in Table 4, permit a reasonable estimate where pleopod stage and temperature are known. These data are applicable to lobsters from approximately 150–900 g. On larger lobsters the pleopods become progressively more opaque and the rates of development are slower than those indicated.

Pleopod stages 3.0 or later give consistent times to ecdysis, but those between 1.0 and 2.5 are less reliable because of the development plateaus that occur during D_0. Oogenesis accounts for some of the protracted Type 3 curves, but males and females both display Type 2 curves of varying duration, and the reasons for this are not clear. Most such plateaus occur at stages 1.5–2.0, and rarely will a lobster remain at stage 2.5 for more than 2 weeks. Once an animal has passed beyond stage 2.5 (into D_1') there will be no further plateaus and proecdysis will proceed at a rate that is regulated by temperature. Ecdysis occasionally occurs in temperatures as low as 1 C.

EXTERNAL CHANGES

Most of the external indications of proecdysis are associated with development of new cuticle (color change) or decalcification (softening of critical areas), and thus occur when the lobster is within a week or so of ecdysis.

According to Barlow and Ridgeway (1969) the lateral margin of the carapace becomes soft in stage D_2 and the abdomen becomes dark purple in D_3. In my experience the lower margin of the carapace becomes progressively darker in color during proecdysis (Fig. 6D) but remains very firm until stage D_3. I have also found that the purple color of the abdomen, which these authors give as a characteristic of D_3, fails to develop in a fair proportion of lobsters approaching ecdysis. Where present it is a reliable indication that ecdysis is imminent, but the absence of this purple color means nothing.

Three external characteristics are useful for predicting ecdysis in lobsters: color and hardness of the lateral margin of the carapace; color of the ventral abdomen; and color and hardness of the merus of the cheliped. These are shown in Fig. 6, and their use in molt prediction is best summarized in a brief key:

1 a. Ventral abdomen white.......Stage C_4
  b. Ventral abdomen pink or mottled purple (proecdysis)..........................2
2 a. Dorsal surface of merus light-colored (Fig. 6C); carapace lateral margin pale blue.... ....approximately 2 weeks to ecdysis
  b. Dorsal surface of merus dark blue........3
3 a. Dorsal surface of merus firm; carapace lateral margin dark-colored but firm (Fig. 6D)...approximately one week to ecdysis 1
  b. Dorsal surface of merus soft (Fig. 6F); carapace lateral margin dark and soft.... ....less than 3 days to ecdysis

The pleopod staging concept described here has been useful for evaluating effects of various experimental treatments on molt physiology, and for predicting the time at which an individual or group can be expected to molt. Previous work on lobster endocrinology and physiology has suffered from uncertainty regarding the molt stage of experimental animals at any point in time. As a consequence there has been a tendency to use ecdysis itself as the assay for molt induction, and ecdysis may not occur for 2 months or more after the inductive event. With pleopod staging it is possible to establish the stage at the start of the experiment, recognize inductive effects when they occur, and monitor subsequent effects on the various substages of proecdysis.

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Growth and Mortality in an Arctic Intertidal Population of *Macoma balthica* (Pelecypoda, Tellinidae)

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GREEN, R. H. 1973. Growth and mortality in an arctic intertidal population of *Macoma balthica* (Pelecypoda, Tellinidae). J. Fish. Res. Board Can. 30: 1345–1348.

In an arctic intertidal environment on Hudson Bay, *Macoma balthica* have a higher growth rate at a tidal level of 1.1 m above mean low water than at the mean low water level, in terms of both length and dry weight. Temperature, rather than food, appears to be the primary proximate factor involved, and summer air temperatures play a major role. The estimated growth rates are comparable to reported growth rates for intertidal *Macoma* populations in Scotland and the Netherlands. A partial life table calculated from the death assemblage indicates that *Macoma* at 1.1 m above mean low water have an annual mortality which increases from about 20% at age 2 to about 50% at age 7 years.

GREEN, R. H. 1973. Growth and mortality in an arctic intertidal population of *Macoma balthica* (Pelecypoda, Tellinidae). J. Fish. Res. Board Can. 30: 1345–1348.

Dans un milieu intertidal arctique de la baie d'Hudson, *Macoma balthica* croît à un rythme plus rapide à 1.1 m au-dessus du niveau moyen de basse mer qu'au niveau moyen lui-même, en termes à la fois de longueur et de poids sec. La température, plutôt que la nourriture, semble être le principal facteur immédiat impliqué, et les températures de l'air en été jouent un rôle majeur. Les rythmes de croissance estimés sont comparables à ceux signalés chez les populations intertidales de *Macoma* en Ecosse et dans les Pays-Bas. Une table partielle de mortalité, calculée à partir d'un assemblage de mortalités, indique que les *Macoma* habitant à 1.1 m au-dessus du niveau moyen de basse mer ont une mortalité annuelle qui augmente d'environ 20% à l'âge de 2 ans à 50% à l'âge de 7 ans.

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LITTLE information is available on growth or mortality rates of arctic intertidal species. Consequently, the theories and general principles relating to arctic shallow water and intertidal ecology are based on very little data. The purpose of this study was to estimate rates of growth and mortality for a common species, *Macoma balthica*, in such an environment and to consider the implications of such rates in relation to comparable data previously reported for non-arctic localities.

Dunbar (1968) summarizes his review of growth rates of marine species in polar regions by citing Dehnel (1955): "Generally the assumption is made that species of marine poikilotherms which inhabit the colder waters of the higher latitudes grow more slowly, grow to larger size, and have a greater longevity than individuals of the same or closely related species from warmer waters." Growth rate tends to decrease with decreasing temperature, and also with decreasing salinity (Vogel 1959; Segerstråle 1960).

The role of food is less clear. For *Macoma*, in particular, Segerstråle (1960) attributes local variation in size in the Baltic Sea to dependence on a heterogeneous substrate for food, but Brafield and Newell (1961) suggest that *Macoma* can feed on suspended organic material at high tide as well as on the surface deposits at low tide. Newell (1965) has shown that deposit-feeding *Macoma* mainly utilize microorganisms attacking carbon compounds which *Macoma* cannot utilize directly, and that microorganism population densities increase as sediment particle size decreases because of the increased surface area.

The Study Area

A study area on the Hudson Bay intertidal 1 mile east of Fort Churchill (58°46′N, 94°02′W) was chosen in July 1970. It is characterized by mixed sand and boulder substrates, and is not directly influenced by Churchill River water; the salinity at high tide on July 9 was 18.1‰. The mean tidal amplitude is 3.35 m and the average slope of the beach is 1 in 125.

The Hudson Bay marine environment is generally considered to be arctic (Hedgpeth 1957; Dunbar 1968). At Churchill the near-shore water is ice-free, on the average, from July 11 to October 23. Mean high tide water temperatures at the mouth of the Churchill River for July, August, September, and October 1971 were, respectively, 2.1, 2.2, 5.0, and 3.9 C. The winter mini-

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mum normal daily low air temperature (in January) is –33 C, but the summer maximum normal daily high air temperature (in late July) reaches 18 C. The combination of low winter temperatures, strong northerly winds, and tidal action results in severe ice abrasion on the intertidal zone.

Methods

At low tide *Macoma balthica* were seen to actively burrow on two sand flats, one at MLW (mean low water) and the other at 1.1 m above MLW. More than 200 m of continuous boulder reefs and tide pools devoid of *Macoma* separate the two sand flats. On July 8, 1970 a square of 9.29 m^2 area on the MLW sand flat was dug out to a depth of 8–10 cm and sieved through a 1-mm screen. All *Macoma* were counted and measured. This was repeated on July 9 for the 1.1-m level sand flat, except that only a 4.65 m^2 area was sampled because the *Macoma* density was higher.

Annual winter rings were present on valves of *Macoma* at both tidal levels. Lengths at consecutive winter rings were measured with vernier calipers and recorded separately for each tidal level, and then used to determine growth curves by the "Walford plot" method of Ford (1933) and Walford (1946). A size series from each tidal level was collected for determination of the length vs. dry weight relation. Sediment samples were collected at each tidal level for analysis of the particle size distributions, which were determined by dry sieving.

Thin sections of *Macoma* shells were examined microscopically to determine the pattern of seasonal growth from the spacing of monthly (lunar tidal) growth lines between annual winter rings.

The site was revisited in 1971. On July 1 four sediment samples were collected from each tidal level to determine sediment organic content. Each 50-g dry weight sample was kept on ice for 4 days, and then dried and combusted in a muffle furnace for 1 hr at 525 C. Organic content was estimated by loss on ignition.

During the period July 1–3 the area around the 1.1-m tidal level sand flat was repeatedly examined for empty but still articulated *Macoma* valves. A partial life table for *Macoma* was calculated from the age distribution of the 101 double valves that were collected.

Results

The mean density of *Macoma* on the MLW sand flat was 6.4/m^2, and on the 1.1 m sand flat 10.1/m^2. The variance among replicate 2.32 m^2 subareas was less than 2% of the mean. *Macoma* were of smaller size at MLW than at 1.1 m (χ^2 (2 df) = 21.6 **), as shown below.

Tidal height	Length (*mm*) <10	10.1–15	15.1–20	Total
1.1 m	14	18	15	47
MLW	44	10	5	59
Total	58	28	20	106

The Walford plot of lengths at consecutive winter rings is shown in Fig. 1. Analysis of covariance indicates that the null hypothesis of similar slopes for the two tidal levels must be rejected (F (1, 52 df) = 11.1 **). For the MLW area the equation of the growth curve is $L_t = 37.3\ (1 - e^{-0.086t})$, where L_t = length in millimeters and t = age in years. Similarly, for the 1.1-m area the equation of the growth curve is $L_t = 21.1\ (1 - e^{-0.309t})$. Both growth curves are shown in Fig. 2. Regressions of *ln* length weight on *In* length were not significantly different for the two tidal levels (F. (1, 36df) = 0.77 ns), and the pooled regression $ln\ W = -9.78 + 3.25\ ln L$ (or $W = 5.67 \times 10^{-5}\ L^{3.25}$) was applied to both. The growth curves in terms of dry weight (Fig. 2) were then calculated from the above equations. Table 1 compares the growth rates at the two Churchill tidal levels with those reported elsewhere.

A thin section of a *Macoma* valve showed five narrow bands between the heavier "winter rings," which corresponds to the number of monthly lunar tidal cycles during the ice-free season. Growth apparently ceases in winter, as has been reported by Lammens (1967) for a Dutch population of

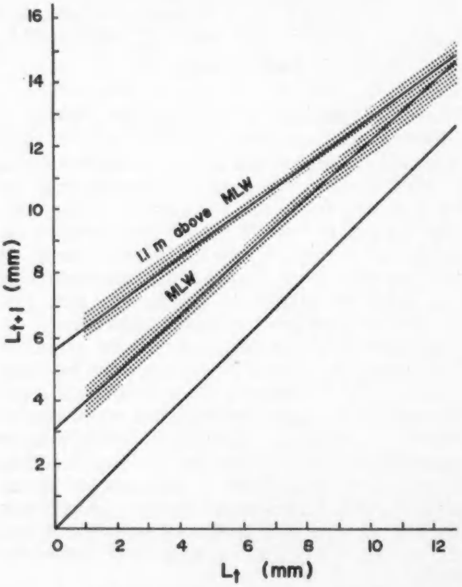

FIG. 1. A "Walford plot" of lengths at consecutive winter rings for *Macoma balthica* from Churchill, Manitoba at two tidal levels. The 95% confidence bands on the regressions are shown.

TABLE 1. Data on growth and maximum age reported for intertidal *Macoma balthica.*

Location	Length (*mm*) at age (*years*) 1	2	3	4	5	Maximum age	Author
Churchill (MLW)	3	6	9	11	13	?	Green
Churchill (1.1 m)	6	10	13	15	17	9–10	Green
Scotland	5	8–9				3	Stephen (1931)
Netherlands	6	12	16	18		7–8	Lammens (1967)

Macoma in which the so-called "winter rings" are actually formed in late summer.

The median sediment particle size at the MLW level was approximately 2 Φ (0.25 mm) and at the 1.1 m level approximately 0.5 Φ (0.71 mm). Sediment organic content at both levels was estimated to be 1.39%, with a pooled standard error of 0.20%.

The life table for *Macoma* at the 1.1-m level from age 2 years, and the survivorship and mortality rate curves, are shown in Fig. 3. The annual mortality rate increases steadily from about 20% at age 2 to about 50% at age 7, resulting in a survivorship curve with increasing negative slope. Comparable data for the MLW *Macoma* population are not available; because of the topography of the beach empty valves at this tidal level are washed out to deeper water.

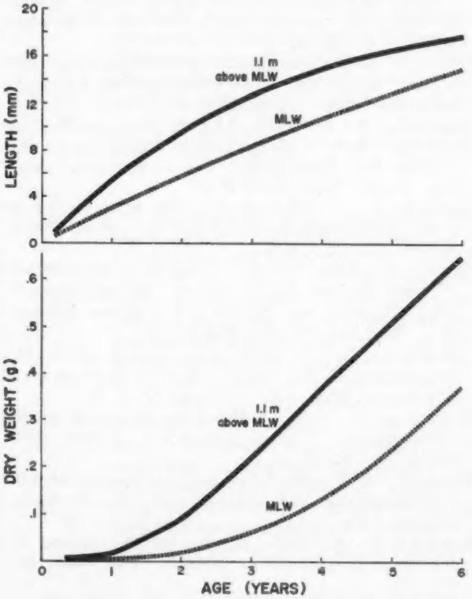

FIG. 2. Estimated length vs. age relation (*upper half*) and dry weight vs. age relation (*lower half*) for *Macoma balthica* at two tidal levels. The straight-line segments do not imply constant growth throughout the year.

Discussion

Growth rates at the 1.1-m tidal level at Churchill (Table 1) are comparable to rates reported for

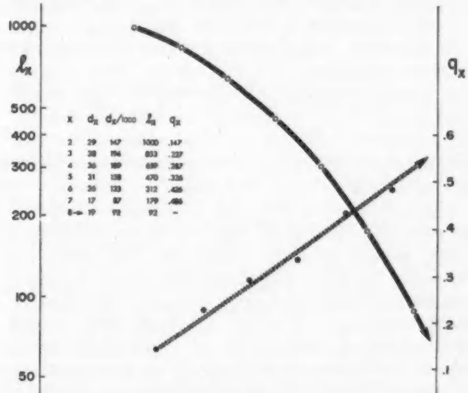

FIG. 3. Estimated life table for *Macoma balthica* at 1.1 m above MLW from age 2 years. Open circles represent the estimated survivorship curve, in numbers surviving (l_x) out of an initial 2-year-old population of 1000. The l_x value is on a logarithmic scale, so that a constant mortality rate would produce a straight line. Solid dots represent the annual mortality rate (q_x), expressed as the fraction dying per year out of the population which started the year alive.

Macoma populations in Scotland (Stephen 1931) and the Netherlands (Lammens 1967), despite colder water, an ice-free season of only 104 days, and a salinity of only 18‰.

The difference in growth rates between tidal levels at Churchill can be explained by the effect of summer air temperature. As Dunbar (1953) points out, the atmospheric climate is an important factor in the special conditions which the intertidal fauna must face. In the study area, the 1.1-m tidal level is exposed to the air about 37% of the time, while the MLW level is exposed briefly only on below-average low tides. Afternoon air temperatures in July and August are often 18 C or more, and the incident solar radiation probably heats the sediments well above this.

The higher growth rate at the 1.1-m tidal level is consistent with the difference between the size-frequency distributions at the two levels. The difference in growth rates must result from differences in either temperature or food. Salinity does not differ. Sediment organic content does not differ, but if food is more abundant at one tidal level then it should be at the MLW level rather than at the 1.1 m level. To the extent that *Macoma* filter-feed at high tide, the MLW population would have more time to feed, and to the extent that *Macoma* deposit-feed, food in the form of microorganisms (Newell 1965) should be more abundant at MLW because of the finer sediments.

I therefore conclude that temperature is the primary proximate factor (Dunbar 1968) causing the higher *Macoma* growth rate at the higher tidal level. Food is likely to be involved only to the extent that feeding activity, along with other biological processes, is probably increased by higher temperatures.

Calculation of a life table (Fig. 3) from the d_x column (distribution of ages at death) assumes a stable population from which ages at death are randomly sampled. However, there is no certainty that these assumptions were satisfied. The life table starts with age 2 years to minimize error caused by the greater probability of small shells being missed or having broken up. The age-frequency histograms for the Dutch population described by Lammens (1967) suggest age-specific mortality rates similar to the Churchill rates, particularly for age 3 years and older.

Dunbar (1968) emphasizes reduced available energy in the arctic marine environment as the important ultimate factor restricting energy expenditure. He believes that "Regulation of any significance in growth rate... appears to be found only where special necessities at the ultimate level exist." I conclude that the results of this study, and of earlier studies by other workers, do not provide evidence for regulation of growth rate related to latitude for intertidal *Macoma balthica*. However, growth rate at different tidal levels in the Churchill population appears to be regulated, and by temperature rather than by available energy.

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Behavioral Responses to Changes in Hydrostatic Pressure and Light During Larval Development of the Lobster *Homarus gammarus*[1]

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ENNIS, G. P. 1973. Behavioral responses to changes in hydrostatic pressure and light during larval development of the lobster (*Homarus gammarus*). J. Fish. Res. Board Can. 30: 1349–1360.

Larvae of the lobster *Homarus gammarus* hatched and reared under laboratory conditions in shallow water responded to changes in hydrostatic pressure in a depth-regulatory manner. Responsiveness to instantaneous pressure increments ranging from 1 to 20 psi increased linearly and there was no threshold of sensitivity within the range tested. Pressure sensitivity was retained throughout larval life up to and including stage IV (megalopa) but responsiveness weakened with age at least up to stage III. Stage IV larvae were highly responsive to pressure changes but stage V (lst juvenile) lobsters were nonresponsive. Older larvae accommodated to sustained pressure more rapidly than younger larvae and larvae quickly became nonresponsive to repeated pressure changes. After being held at high pressure, larvae responded to slight pressure decreases by downward movement even though still held at pressures to which they would initially respond by vigorous upward movement. Larvae were more responsive to pressure in overhead light than in darkness but light intensity had no apparent effect on the initial response nor on the rate of accommodation to sustained pressure, but in darkness the initial response was slower. Responsiveness to sudden changes in light intensity was much less marked than to pressure changes and it also weakened with age. In the sea older larvae showed a stronger tendency for downward movement when released at the surface and a decreasing tendency for upward movement when released at depths of 25 ft (7.61 m) or more. The average rate of upward movement decreased over a 5-min period and there was no consistent difference in this rate or in the rate at which it decreased when larvae were released at different depths. The average rate of upward movement tended to decrease with age.

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Des larves de homard *Homarus gammarus* incubées et élevées au laboratoire en eau peu profonde, réagissent aux changements de pression hydrostatique en changeant de profondeur. La réponse à des augmentations instantanées de pression allant de 1 à 20 livres par pouce carré augmente linéairement, et il n'y a pas de seuil de sensibilité dans l'intervalle étudié. La larve conserve sa sensibilité à la pression jusqu'au stade IV (mégalope), mais le degré de réponse diminue avec l'âge, au moins jusqu'au stade III. Les larves au stade IV sont très sensibles aux changements de pression, et il semble y avoir augmentation de sensibilité à la pression au moment de la mue qui précède le stade IV. Les homards au stade V ne semblent pas sensibles aux changements de pression. Le taux d'accomodation à une pression soutenue augmente avec l'âge, et les larves deviennent rapidement insensibles à des changements répétés de pression. Après avoir été maintenues à une haute pression, elles répondent à de légères diminution de pression par des déplacements vers le bas, même si elles sont encore maintenues à des pressions auxquelles elles auraient répondu initialement par de vigoureux mouvements vers le haut. Les larves sont plus sensibles à la pression lorsque le dessus des bassins est éclairé qu'à l'obscurité, mais l'intensité lumineuse n'a pas d'effet apparent sur la réponse initiale, non plus que sur le taux d'accomodation à une pression soutenue, mais dans l'obscurité, la réponse initiale est plus lente. La sensibilité à des changements soudains d'intensité lumineuse

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[1] This study was done at Port Erin while the author was on educational leave from the Fisheries Research Board of Canada and is part of a research program leading to the degree of Doctor of Philosophy at the University of Liverpool.

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est beaucoup moins marquée que la sensibilité à des changements de pression, mais elle diminue également avec l'âge. Dans la mer, les larves plus âgées démontrent une plus forte tendance à se diriger en profondeur lorsque libérées à la surface, et une tendance moins forte à se diriger vers le haut lorsque libérées à des profondeurs de 25 pieds (7.61 m) ou plus. La vitesse moyenne de migration vers le haut diminue après 5 mn, et il n'y a pas de différence uniforme entre cette vitesse et le taux de diminution lorsque les larves sont libérées à des profondeurs différentes. La vitesse moyenne de migration vers le haut a tendance à diminuer avec l'âge.

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HARDY and Bainbridge (1951) found that decapod crustacean larvae were sensitive to small pressure changes and responded to increased pressure by moving upwards and to decreased pressure by moving downwards. Barosensitivity is now known to be a common depth-regulatory mechanism in planktonic animals (Knight-Jones and Morgan 1966; Knight-Jones and Qasim 1955; Rice 1964, 1967). Rice categorized the main types of pressure responses in planktonic animals. Pressure responses in stage I zoeae of all decapod crustaceans examined were orientated to light, but megalopa of *Carcinus maenas* and *Macropipus* sp. were oriented to gravity. Stages I and IV larvae of the lobster, *Homarus gammarus*, (= *H. vulgaris* H. Milne-Edwards) were oriented to light (Rice 1967).

Homarus gammarus larvae are very rarely taken in plankton collections (D. I. Williamson personal communication) and their distribution in nature is virtually unknown. The purpose of this study was to examine the role of pressure sensitivity as a depth-regulatory mechanism throughout the larval life of the species and from this to obtain clues to their distribution in nature.

Materials and Methods

Ovigerous lobsters with eggs nearly ready to hatch were obtained from local fishermen and held in tanks of running sea water outside the laboratory. Larvae were obtained from several different broods throughout the period May–August 1972. They hatched at night and the following morning those to be used immediately in experiments were taken directly from the hatching tank and the remainder put in 45-liter polyethylene containers. The numbers of larvae initially in these rearing containers averaged about 6–7 larvae/liter. They were fed *Artemia* nauplii. Each day the water was changed and debris and dead larvae were removed by siphoning. Even with high *Artemia* concentration cannibalism was high, especially after most of the larvae had molted into stage II. To get stage III and IV larvae, 8–10-day-old stage II larvae were held individually in 2.5-liter white polyethylene buckets. The larvae were exposed to natural illumination. Mortality through stage II and later stages was very high due mainly to algal growth on the larvae, however survivors appeared to be healthy.

The experimental column was a Plexiglass cylinder, 78 cm long, 6-cm internal diameter, and walls 4.5 cm thick. It was fitted with a collar at the top to which the cover could be tightly bolted. Grooves were cut in the collar and in the cover between which an 0-ring was fitted so the column could be pressure sealed. It was connected to a cannister through a hole in the cover by 5-mm thick rubber hose with 6-mm internal diameter. The cannister had a screw-on top with an air pressure gauge graduated in 2½ psi and an automobile tubeless tire valve (1 atm (1000 mb) = 14.7 psi). Air pressure was built up in the cannister using an automobile tire pump. Pinchcock clamps were fitted so that the pressure could be applied and released instantaneously.

Experiments were carried out in darkness and in vertical overhead light of different intensity. When experiments were done in darkness the lower three-quarters of the column was blacked out and the number of larvae in the top one-quarter was observed using a dim red light which was left on for only 3 or 4 sec. Vertical overhead light was provided by a microscope lamp on top of the column which gave a unidirectional parallel beam of bright white light from a 15 w bulb. Various light intensities were obtained by removing a 1.5-mm thick piece of frosted glass to give brighter-light (very bright white light) or by placing one (bright green light), two (medium green light), or three (dim green light) pieces of translucent green polyethylene in front of the frosted glass to give light of progressively lower intensity. Relative differences in light intensity were recorded with a Sekonic Auto-lumi L-86 photo exposure meter with a Schott VG9 filter in an underwater housing. The exposure value readings for the various light intensities were within the range obtained to depths of 40 ft (12.2 m) in the sea during daytime.

A 2–3 C temperature difference between top and bottom of the column developed after using bright white light about 1½ hr. Most experiments using overhead light were shorter than 1 hr and the slight temperature gradient had no apparent effect on the movement of larvae in the column in response to changes in pressure and light intensity. Only healthy-looking, vigorous larvae were used and after each experimental run all were discarded. In the pressure response experiments 10 larvae were used in each run except with stages III, IV, and V where individual larvae were used. The responses to changes in light intensity were observed for stage I and II larvae only and 20 larvae were used in each run. With very few exceptions the result of each experimental condition represents the average of at least three runs. Numbers of larvae in the top quarter of the column were observed before and after pressure changes and these were used to illustrate the response. The response to changes in light intensity was much less vigorous and clear-cut and it was illustrated by the numbers of larvae in the top half.

Larvae about the same age and taken from the same batches as those used in the experiments were also released in the sea and observed by divers. These larvae were taken from the rearing containers about 30 min before the start of the dive and held individually in sealed 125-ml glass bottles of sea water. At the start of the dive, light and temperature readings were taken at the surface and at 10-ft (3.0-m) intervals to a depth of 40 ft (12.2 m). After about 15–45m in of temperature acclimation larvae were released individually at the bottom at about 30–40 ft (9.2–12.2 m), at 25 ft (7.6 m), at 10 ft (3.0 m), and at the surface. Larvae were followed for 5–10 min and their position, usually at 1-min intervals after release, was recorded. A Bouyee Fenzy life vest allowed the diver to maintain neutral buoyancy at all depths thus avoiding vigorous swimming movements near the larvae.

Results

EFFECT OF PRESSURE CHANGES IN DARKNESS

Stage I larvae up to 5-days-old were exposed to pressures ranging from 1 to 20 psi in darkness (Fig. 1). At each age more larvae were swimming in the top quarter of the column when exposed to the higher pressures. There was no threshold of sensitivity within the range of pressures to which the larvae were exposed and responsiveness to pressure increased linearly with the magnitude of the pressure applied. When 8–11-hr-old larvae were allowed to feed for ½ hr in highly concentrated *Artemia* before being put into the experimental column, fewer of them responded to the pressure increases. Responsiveness to pressure increases diminished during the first day but there was very little difference between 1- and 5-day-old larvae. The rate at which pressure was applied made very little difference to the number of larvae in the top quarter when the pressure had been reached (Fig. 2).

Accommodation (downward movement in the column following the initial upward movement in response to the pressure increase), when pressure was sustained at 5 and 20 psi, was very slow and in both instances only a few larvae moved out of the top quarter during a long period of pressure exposure (Fig. 3). When the pressure was dropped to zero (= ambient atmospheric) downward movement was fairly rapid.

Accommodation (lack of upward and downward movement) to pressure pulses occurred fairly rapidly (Fig. 4). When the pressure was released after the first pulse, downward movement of larvae was considerable, especially at the higher pressures, but the number of larvae responding to successive pulses decreased considerably and very few larvae responded to the third and later pulses compared to the first. There was a marked response to a sudden increase to 25 psi after six pulses of 5 psi but not after the pulses of higher pressures. Other experiments also showed that response to pressure changes depended to a large extent on previous pressure experience, and larvae responded to slight

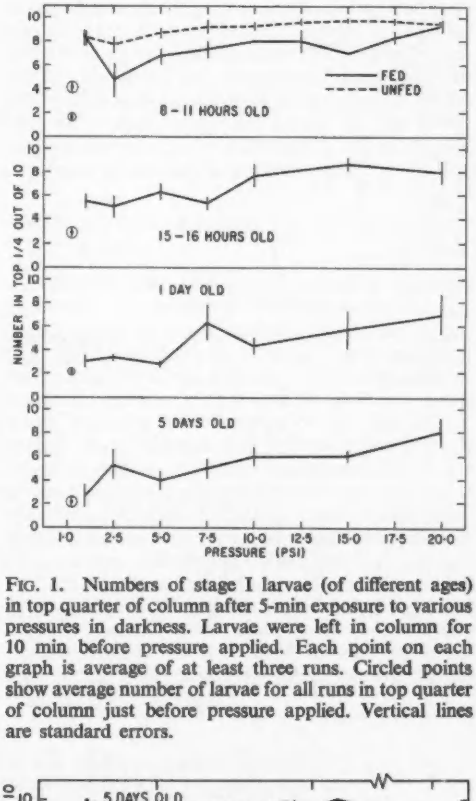

FIG. 1. Numbers of stage I larvae (of different ages) in top quarter of column after 5-min exposure to various pressures in darkness. Larvae were left in column for 10 min before pressure applied. Each point on each graph is average of at least three runs. Circled points show average number of larvae for all runs in top quarter of column just before pressure applied. Vertical lines are standard errors.

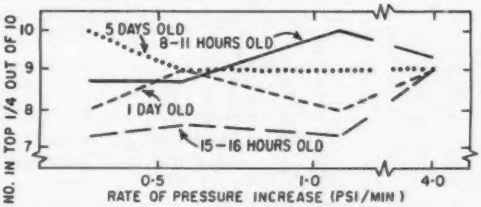

FIG. 2. Numbers of stage I larvae (of different ages) in top quarter of column when 20 psi applied at different rates in darkness. (For 1- and 5-day-old larvae only one run each.)

pressure drops by moving downward even though still being held at pressures to which they would initially respond by vigorous upward movement (Fig. 5). The length of time between two successive pulses and the duration of the first pulse had no apparent effect on the numbers of larvae responding to the second pulse (Table 1). A series of control runs was made with the first experiments and at zero pressure there were very few larvae in the top quarter of the column and only slight changes in numbers over a 75-min period. The response to pressure changes was so clear-cut that control runs with each series of experiments were considered unnecessarily time consuming.

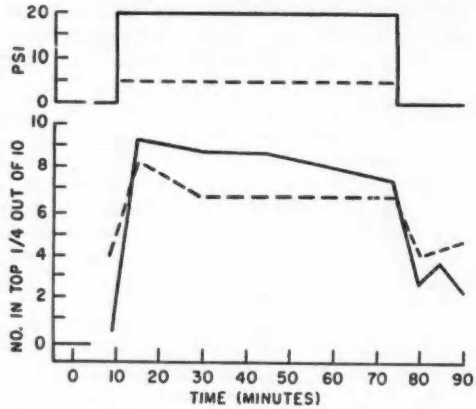

FIG. 3. Numbers of 8–11-hr-old larvae in top quarter of column when pressures of 5 and 20 psi sustained in darkness.

EFFECT OF PRESSURE CHANGES IN OVERHEAD LIGHT

When experiments were done in overhead light it was clearly seen that the larvae responded immediately to a sudden increase in pressure, and usually all the larvae that were to move up into the top quarter of the column had done so in less than 1 min. Upward movement was usually accomplished by increased beating rate of the swimming appendages (exopodites of thoracic appendages), but occasionally some larvae (especially stage II larvae) used short bursts of rapid tail flexes.

In bright green light more larvae remained in the top quarter of the column before pressure was applied than when left in darkness. There was much less difference in numbers of larvae responding as the pressure applied was increased

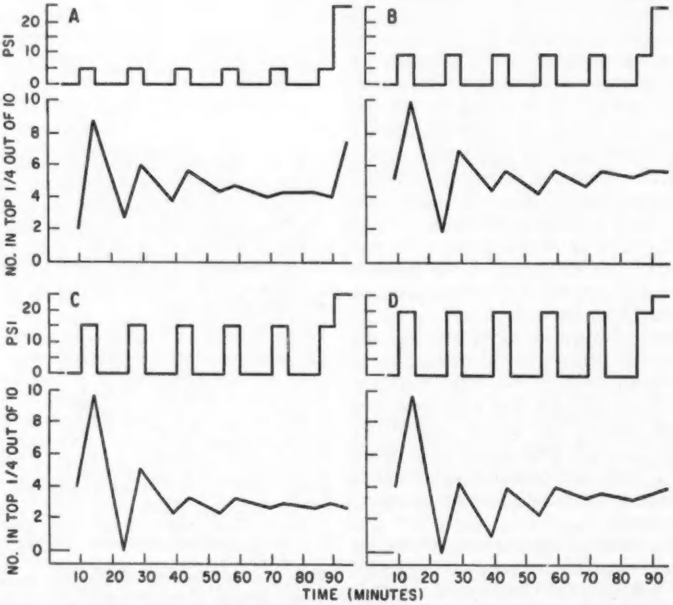

FIG. 4. Numbers of 8–11-hr-old larvae in top quarter of column when pressure of different magnitude pulsed in darkness.

(Fig. 6) than when similar experiments were done in darkness (Fig. 1). Evidently larvae are more responsive to pressure increases, particularly small increases, in overhead light than in darkness. At each age some larvae that moved up into the top quarter during the first minute of pressure exposure had moved down after only 5 min. This rapid accommodation was particularly evident for 5-day-old stage I larvae. After being put into the column at the start of an experiment and during the interval before pressure was applied, older larvae dispersed to the lower part of the column more rapidly than younger larvae (Fig. 7), and also as age increased fewer larvae responded to pressure increases. For all ages at both 5 and 20 psi some larvae that moved up into the top quarter of the column when the pressure was applied accommodated to the pressure and moved down during the short period (20 min) of pressure exposure. Dispersal to the lower part of the column when the pressure was released was more rapid, particularly at the higher pressure, than at the start of the experiments before the larvae had been exposed to the increased pressure (Fig. 7).

Insufficient numbers of stage IV (megalopa) and stage V (lst juvenile) were available to obtain adequate comparisons between their pressure responses and those of earlier stages, but two specimens in stage IV which were tested in overhead light showed definite pressure sensitivity, with upward swimming after sudden pressure increase and gradual sinking following pressure release. They appeared to be more sensitive to pressure changes than stage III larvae. Stage IV larvae are certainly more efficient swimmers than earlier stages and there may be an increase in pressure sensitivity at the metamorphosis that occurs during the molt into stage IV. The one specimen in stage V observed in the laboratory, although a very capable swimmer, showed no sensitivity to pressure changes of 20 psi, and it seems likely that there is a loss of the type of pressure response present in the larval stages during the molt into stage V which enables this stage to become completely benthic.

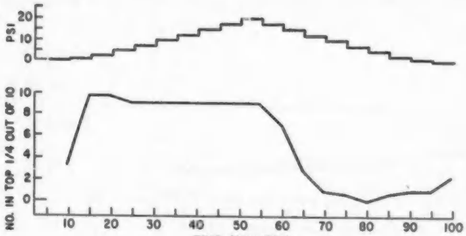

FIG. 5. Numbers of 8–11-hr-old larvae in top quarter of column as pressure increased and decreased slowly.

EFFECT OF PRESSURE CHANGES AT DIFFERENT LIGHT INTENSITIES

Larvae of various ages were exposed to sustained pressures of 5 and 20 psi in darkness and in overhead light of various intensities (Fig. 8). The initial response of 8–11-hr-old larvae to both pressures was complete in all lighting conditions and accommodation was very slight. In older larvae the initial response and the rate of accommodation varied under different lighting conditions at both pressures but the variation was inconsistent. Older larvae accommodated more rapidly, particularly at the lower pressure. In darkness and in dim green light there were always fewer larvae in the top quarter of the column just before the pressure was applied, but although there was in some instances variation in the amount of downward movement following pressure release there again was no consistent pattern. Except for 8–11-hr-old larvae, the initial response to both pressures in darkness was slower than in overhead light.

TABLE 1. Numbers of 8–11-hr-old larvae in top quarter of column at 20 psi (a) after 5, 15, and 25 min at 0 psi following 10-min exposure to 10 psi and (b) after 10 min at 0 psi following 5, 15, and 25 min exposure to 10 psi.

a			b		
Time at 10 psi (*min*)	Time at 0 psi (*min*)	No. (mean)	Time at 10 psi (*min*)	Time at 0 psi (*min*)	No. (mean)
10	5	2,3,4(3)	5	10	3,4,2(3)
10	15	2,3,4(3)	15	10	4,7,3(4.7)
10	25	0,4,0(1.3)	25	10	4,2,5(3.7)

Effect of Sudden Changes in Light Intensity

After some time in darkness the initial response of 8–11-hr-old larvae to overhead light was generally very slow upward swimming towards the light source (positive phototaxis). The level of the response appeared to depend on the light intensity (Fig. 9). More larvae responded to bright light than to dull light and fewer moved away from brighter light following the initial response. As light intensity was increased at regular intervals, larvae continued to move upward toward the light source and as the light intensity was decreased they gradually moved downward away from the light.

Younger larvae were more sensitive to a change in light intensity, and more responded by moving upwards toward the light source (Fig. 10). At zero pressure more newly hatched larvae swam in the top half of the column than older larvae and fewer newly hatched and 8–11-hr-old larvae moved downward during $\frac{1}{2}$-hr exposure to overhead light. At 5 psi there were more larvae in the top half of the column throughout the experiments, except for 8-day-old stage II larvae where there was little difference.

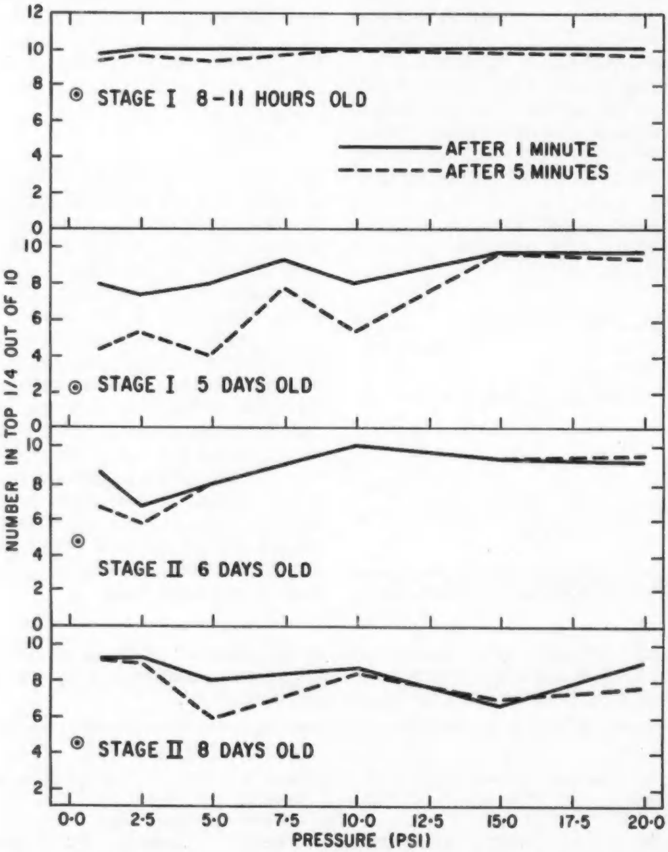

FIG. 6. Numbers of stage I and II larvae (of different ages) in top quarter of column after 1- and 5-min exposure to various pressures in overhead bright green light. Larvae were left in column for 10 min before pressure applied. Each point on each graph is average of three runs. Circled points show average number of larvae for all runs in top of column just before pressure applied.

Observations on Larvae Released in the Sea

When released in the sea there was considerable variation in the movement of individual larvae of the same age, and there was no obvious depth selection by larvae of the same age released at different depths on the same day. Stage I larvae 15–16-hr-old released at the surface tended to remain close to the surface and those released at various depths tended to move surfaceward, but there was considerable variation in the rate of upward movement by larvae released at the same depth. The maximum rate of upward movement observed for larvae of this age was 13 ft (4 m)/minute, however, larvae released near the bottom in depths of 30–40 ft (9–12 m) generally did not swim directly all the way to the surface. In older larvae the tendency to swim downward after being released at the surface was much greater (Table 2), and although there was generally upward movement after being released at depths of 25 ft (7.6 m) or more the tendency to swim upwards and the average rate of upward movement were both lower in older larvae. In larvae aged 35–40 hr (stage I) the maximum rate of downward movement observed after being released at the surface was 2.4 ft (.73 m)/minute and the maximum rate of upward movement observed was 10 ft (3.05 m)/minute. For 5-day-old stage I larvae these rates were 5 ft (1.5 m) and 8 ft (2.4 m)/minute, respectively, and for 8-day-old stage II larvae they were 8 ft (2.4 m) and 10 ft (3.0 m)/minute. The average rate of upward movement was usually greatest during the first minute after release and tended to decrease over a 5-min period (Table 3). The average rate of upward movement showed no consistent variation with depth of release nor did the tendency for this rate to decrease.

Releases of specimens in stages III, IV, and V were too few for adequate comparisons with earlier stages and the stage IV and V specimens had previously been used in laboratory experiments. Stage III larvae, however, showed a marked tendency to move downward when released at the surface and even at depths as great as 25 ft (7.6 m), but when released at depths greater than 30 ft (9.0 m) the tendency was to move up. The maximum rate of upward movement observed was 10 ft (3.0 m)/minute and 7 ft (2.0 m)/minute was the maximum rate of downward movement observed. The two stage IV larvae released (one was recaptured after being released at the surface and released again at the bottom) showed a marked tendency to remain very close to the surface and to move up when released close to the bottom. One released at 40 ft (12.0 m) moved all the way to the surface

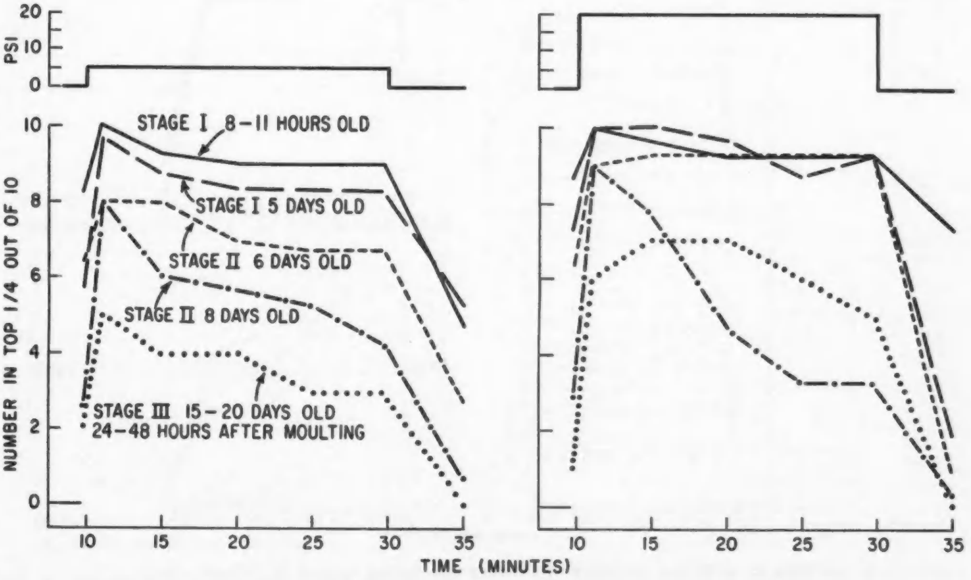

FIG. 7. Numbers of larvae of different ages in top quarter of column when pressures of 5 and 20 psi sustained in overhead bright green light. (Lines for stage III larvae represent observations on 10 individual larvae.)

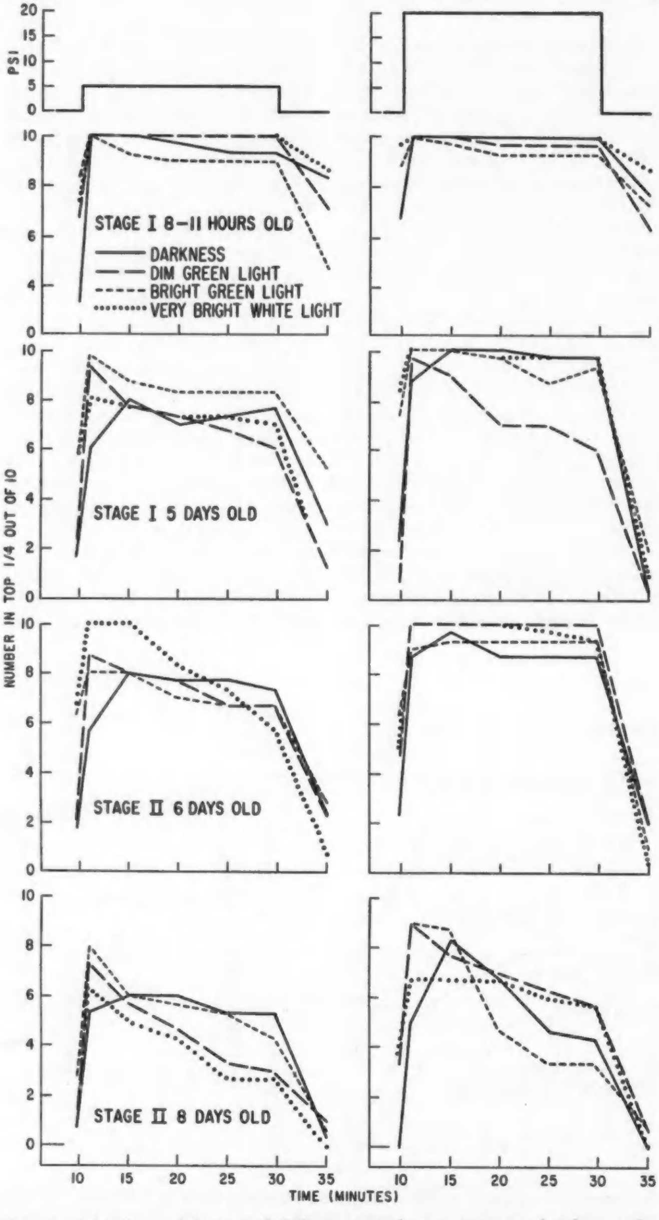

FIG. 8. Numbers of larvae of different ages in top quarter of column when pressures of 5 and 20 psi sustained at different light intensities.

in 5 min, and the maximum rate of upward movement during a 1-min period was 13 ft (4.0 m). The one stage V specimen released at the surface sank slowly to 20 ft (6.0 m) after 6 min, then swam slowly up to 15 ft (4.6 m), then started to sink slowly again and after 10 min was at 18 ft (5.5 m). When the same specimen was recaptured and released at the bottom it crawled over the bottom for several minutes, then took shelter under a small stone where it remained for several more minutes.

Discussion

This appears to be the first attempt at a comprehensive study of pressure sensitivity and associated behavior throughout the larval life of any one species of decapod crustacean. Caution must be used in interpreting the results of the study in terms of the behavior of larvae living in nature. In the laboratory, pressure changes were instantaneous, but under natural conditions pressure changes would be considerably slower as the larvae move up or down in the water column. However, in the laboratory they responded to pressure changes as low as 1 psi, equivalent to a change in depth of about .7 m which they are capable of swimming in a very short time in nature. Also the larvae were reared at almost constant (near ambient atmospheric) pressure and therefore were unaccustomed to pressure changes before the experiments began except those to which they were

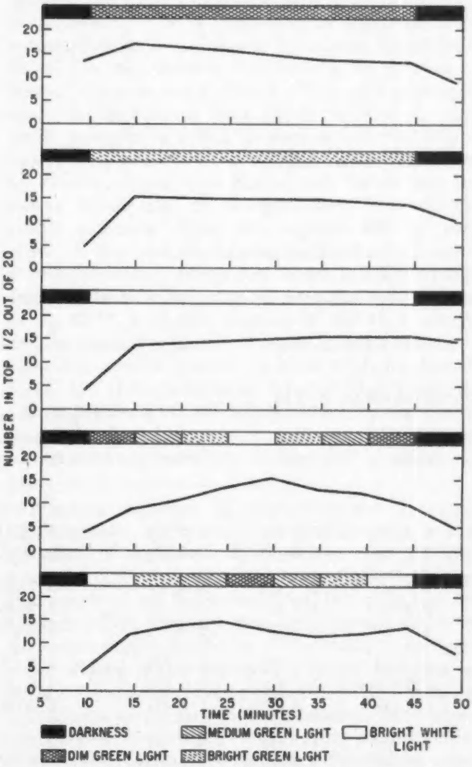

FIG. 9. Numbers of 8–11-hr-old larvae in top half of column with sudden changes in light intensity of different magnitude and with changing light intensity.

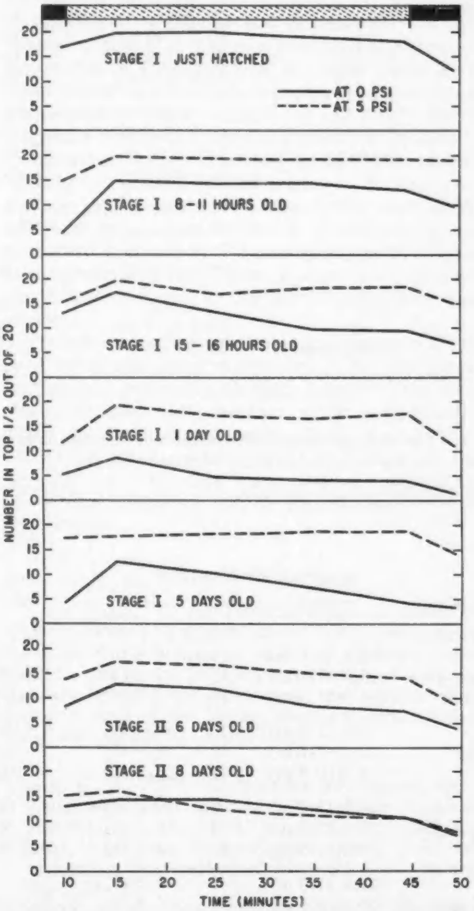

FIG. 10. Numbers of larvae of different ages in top half of column at a sustained light intensity with pressure at zero and at 5 psi.

exposed as eggs, before the female lobster was caught in the fishery. They accomodate to sustained pressure and become nonresponsive to repeated rapid pressure changes so that their response to a pressure change is greatly influenced by their previous pressure experience. Responsiveness to pressure and changes in light intensity decreased, indicating an increasing tolerance for deep water, as larvae got older. In the sea some larvae swam down very quickly and showed no response to increasing pressure, and this tendency was greater in older larvae. The few observations on stage

TABLE 2. Direction of movement of larvae of various ages 5 min after release in the sea in relation to depth of release.

Age of larvae	Depth of release	No.	No. moving up	No. moving down	No. no movement
15–16 hr	Surf.	12	–	3	9
	10 ft (3.0 m)	10	10	–	–
	25 ft (7.6 m)	12	12	–	–
	36 ft(11.0 m)	13	13	–	–
34–40 hr	Surf.	12	–	9	3
	10 ft (3.0 m)	12	9	3	–
	25 ft (7.6 m)	10	10	–	–
	34 ft(10.4 m)	15	14	–	1
5 days, stage I	Surf.	9	–	7	2
	10 ft (3.0 m)	5	2	3	–
	25 ft (7.6 m)	6	4	–	2
	37 ft(11.3 m)	10	8	–	2
8 days, stage II	Surf.	13	–	9	4
	10 ft (3.0 m)	8	3	5	–
	25 ft (7.6 m)	10	7	3	–
	37 ft(11.3 m)	14	14	–	–

TABLE 3. The average upward movement in five 1-min intervals after release and average total upward movement after 5 min for larvae that moved up after being released in the sea.

			Avg distance moved up in ft in					
Age of larvae	Depth of release	No.	1st min	2nd min	3rd min	4th min	5th min	Avg total upward movement after 5 min
15–16 hr	10 ft (3.0 m)	10	6.6 (6)*	2.7 (3)	–	–	–	8.3 (7)
	25 ft (7.6 m)	12	7 (8)	5.6 (6)	6.3 (7)	5.2 (4)	3.5 (4)	19.1(11)
	36 ft(11.0 m)	13	3.7 (7)	4 (7)	5.2 (8)	4.4 (7)	2.7 (7)	20.2(13)
34–40 hr	10 ft (3.0 m)	12	4 (7)	4.1 (6)	1.5 (4)	2 (2)	–	5.7 (8)
	25 ft (7.6 m)	10	6 (8)	5 (8)	5.1 (8)	2.3 (6)	1.7 (4)	15.5(10)
	34 ft(10.4 m)	15	5.1(10)	4.7(10)	4.3(10)	3.3(10)	2.9(10)	18 (15)
5 days, stage I	10 ft (3.0 m)	5	0 (2)	1 (2)	2 (2)	2 (1)	0 (1)	4.5 (2)
	25 ft (7.6 m)	6	2 (4)	2 (4)	1.3 (3)	2 (2)	2 (2)	9.8 (6)
	37 ft(11.3 m)	10	4.2 (6)	1.3 (6)	1.3 (6)	1.4 (7)	1.2 (5)	8.9(10)
8 days, stage II	10 ft (3.0 m)	8	5.5 (2)	–	1 (2)	1 (1)	0 (1)	5.5 (2)
	25 ft (7.6 m)	10	1.1 (6)	2.5 (6)	3.4 (5)	2.6 (6)	2.6 (6)	10.1 (6)
	37 ft(11.3 m)	14	4 (13)	1.9(12)	1.9(13)	1.1(12)	2.1(13)	11.6(14)

*Number in parentheses is number of observations.

IV larvae, although insufficient for adequate comparisons with earlier stages, indicate that pressure sensitivity as a depth-regulatory mechanism is retained throughout the complete larval life of the lobster, but observations on the lst juvenile stage (= stage V) indicate that it is not present in this stage. It is this stage that becomes completely benthic, at least in *H. americanus* (Herrick 1911), and obviously pressure responses of a depth-regulatory nature would be much less useful in this stage.

Larvae of *H. gammarus* are very rarely taken in plankton samples; those that have been taken were in very small numbers and mostly stage IV (Scott 1905; Jackson 1913). In contrast, larvae of *H. americanus* of all stages are commonly taken in large numbers in the plankton (Templeman 1937, 1939; Templeman and Tibbo 1945; Scarratt 1964). The apparent difference in larval distribution between the species may be explained by differences in abundance but a difference in behavior also seems possible. *H. gammarus* larvae may spend their larval life very close to the bottom. *H. gammarus* larvae hatch at night (Ennis 1973), and although newly hatched larvae were highly sensitive to very small pressure increases in darkness in the laboratory, it is possible that embryos become sensitive to pressure some time before they hatch and in nature larvae may be accommodated to a considerable pressure when they emerge and do not swim to the surface. Larvae hatched and reared in the laboratory sometimes swam quickly to the surface after being released in nature at depths of 30–40 ft (9–12 m); whether or not they would do the same if released at night is not known — some also stayed close to the surface when released there, but it is possible that larvae that hatch in nature, if they go to the surface at all, do not spend very long there before moving close to the bottom where they are not likely to be taken by plankton gear.

Pressure responses of *Daphnia magna* are very much greater under dark conditions than in the presence of overhead illumination, even of low intensity (Lincoln 1970, 1971). In *Daphnia magna* the response to light overrides the response to pressure. This suggests that the pressure sense is dominant during the hours of darkness, or perhaps more strictly when the light intensity is below a certain minimum level (Lincoln 1970). Such a mechanism would prevent the animals from wandering outside their depth range during dark periods. This was not found to be the case with lobster larvae, where no consistent difference was found in responsiveness to pressure at different light intensities including darkness, except that in darkness the response was slower. Endogenous activity rhythms synchronized by light/dark cycles have been shown to be important in diurnal vertical migration of a variety of planktonic crustacea (see Naylor and Atkinson 1972 for review). Most observations have been made on copepods and a smaller number on amphipods, isopods, and cumaceans but as yet this phenomenon has not been demonstrated in decapod larvae. Limited observations during the present study showed no indication of endogenous activity rhythms in recently hatched lobster larvae. It is possible that these larvae may not have experienced sufficient light/dark cycles for an activity rhythm to have become entrained or, following a suggestion by Naylor and Atkinson (1972) for plankton generally, pressure may be important in synchronizing these rhythms in lobster larvae and these larvae were hatched and reared at near ambient atmospheric pressure. Templeman and Tibbo (1945) suggested a diurnal vertical migration for *H. americanus* larvae controlled entirely by light/dark cycles, with larvae tending to concentrate at or near the surface during daylight, except under conditions of bright sunshine which tended to repel the larvae and drive them from the surface layers. At night there appeared to be a gradual dispersal to greater depth and a return to the surface the following morning.

Pressure sensitivity appears to be more important as a depth-regulatory mechanism in *H. gammarus* larvae than sensitivity to light, however they evidently do not depth-regulate within well-defined limits by the pressure sense alone. Endogenous activity rhythms, synchronized or reinforced by pressure and light/dark cycles may be important in vertical migration or in maintaining vertical distribution.

Acknowledgments

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OBITUARY

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1897-1972

Dr Ernest Hess died in Kitchener, December 1, 1972.

Dr Hess received his preliminary training in bacteriology in his native Switzerland. On arrival in Canada he was fortunate to secure a place in the laboratory of Dr G. B. Reed, Professor of Bacteriology in the Medical School of Queen's University as Dr. Reed's interests embraced the whole field of microbiology. Dr Hess received the degree of Master of Arts in bacteriology in 1925.

In the same year he became bacteriologist at the newly established Fisheries Experimental Station of the Biological Board of Canada (later the Fisheries Research Board) at Halifax. Almost at once he started work towards the degree of Doctor of Philosophy at McGill University, choosing as the subject of his thesis the growth of bacteria normally contaminating fish, especially at temperatures in the region of 0 C. This study formed the basis of work both in the Halifax laboratory and elsewhere and has had a very important bearing on steps which subsequently brought about a marked improvement in the quality of fish both at sea and ashore.

But Dr. Hess had greater interest in people than in impersonal studies in the laboratory. The main source of income for most shore fishermen has always been lobster, and in the early days of Dr Hess' work, the majority of the catch was canned. He worked with the canners of the Maritimes and because of his teaching and precept the pack of canned lobsters became of uniformly high quality.

The work with canned lobster and the inspection of fish for overseas markets pointed to the necessity of laboratory control of all fish inspection carried on by the Department of Fisheries. When a laboratory was set up in 1947, first at the Fisheries Research Board Laboratory and later in its own building, Dr Hess was the obvious man to head it and to coordinate the work of the fish inspectors and the laboratory staff. The smooth functioning of this laboratory is due largely to the pioneering work of Dr Hess.

In 1949 he joined the Fisheries Division of the Food and Agriculture Organization as Senior Technologist and became Chief Technologist in 1953. While with FAO his interests covered technology of the whole world fishery, although the problems of the emerging nations in Asia and Africa took most of the attention of his section. In 1958 he reached retirement age but instead of a quiet retirement life in Canada, he immediately accepted a post with the Government of Canada to aid in the development of fisheries of the Caribbean area. He remained on this assignment until 1962.

In the mid-1960s he went to Uganda to investigate the large scale utilization of fish from Lake Victoria under the terms of a Canadian Executive Services Overseas project.

While at Queen's University he married Muriel MacLeod who shared his busy life and accompanied him on his many wanderings. They were accomplished singers and music was very important to them. He is survived by his wife and two sons, David of Montreal, Que., and Ian of Sydney, N.S.

S. A. Beatty

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NOTES

Probable Causes for the 1972 Red Tide in the Cape Ann Region of the Gulf of Maine[1]

HUGH FRANCIS MULLIGAN

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MULLIGAN, H. F. 1973. Probable causes for the 1972 red tide in the Cape Ann region of the Gulf of Maine. J. Fish. Res. Board Can. 30: 1363–1366.

Hydrographic data and spatial, temporal, and vertical distributions of *Gonyaulax tamarensis* are presented from the vicinity of Cape Ann, Massachusetts in summer of 1972. When considered together with available meteorological records, these data provide information on probable causes and development of the September 1972 red tide bloom in the Gulf of Maine. An upwelling of deep water, development of a "seed" population of *G. tamarensis* during unusually dry weather in August, and heavy rainfall in September are suggested as the three causative factors.

MULLIGAN, H. F. 1973. Probable causes for the 1972 red tide in the Cape Ann region of the Gulf of Maine. J. Fish. Res. Board Can. 30: 1363–1366.

Nous présentons ici des données hydrographiques ainsi qu'un aperçu de la distribution dans l'espace, dans le temps et en profondeur de *Gonyaulax tamarensis* dans le voisinage du cap Anne, Massachusetts, au cours de l'été 1972. Mises en parallèle avec les observations météorologiques disponibles, ces données nous éclairent sur les causes probables et sur l'évolution de la "marée rouge" de septembre 1972 dans le golfe du Maine. Une remontée d'eaux profondes, le développement d'une population de "semence" de *G. tamarensis* au cours d'une période de sécheresse inusitée en août et des pluies abondantes en septembre seraient les trois facteurs responsables.

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DURING September 1972, a bloom of the dinoflagellate, *Gonyaulax tamarensis*, occurred from Massachusetts to Maine. *Gonyaulax* is concentrated by filter-feeding shellfish which when eaten by humans in sufficient quantities results in paralytic shellfish poisoning (Prakash 1967). Clam flats contaminated with this dinoflagellate were closed in Massachusetts, then several days later in New Hampshire and southern Maine when their clams also became toxic.[2] The red tide created severe economic problems for the shellfish and finfish industries of New England.

The occurrence of *G. tamarensis* has been noted repeatedly in the Gulf of Maine (Prakash 1963; Gran and Braarud 1935; Lillick 1937). Gran and Braarud (1935) indicate it as a common coastal form in the Bay of Fundy from May to September reaching populations of 2800 cells/liter. They also reported its presence at one station in April. Lillick (1937) collected it south of the Gulf of Maine, in the Woods Hole region, from July to September in 1935 (maximum abundance 1300 cells/liter on September 3) but was unable to find it in 1936. Burkholder (1933) did not locate it in a June 28–August 28, 1930 study of phytoplankton of Penobscot Bay and Frenchman Bay, Maine. The organism was not reported by Conover (1956), Lackey (1963), Pratt (1959), Riley (1952), or Smayda (1957) in their phytoplankton studies along the east coast of the United States from New York to Rhode Island. Prakash (1967) stated that *G. tamarensis* never occurred in enough abundance south of Maine to cause shellfish poisoning.

Because inshore surface waters of the Gulf of Maine contain specimens of *G. tamarensis* from April to September (Gran and Braarud 1935), it

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[1] Published with the approval of the Director of the University of New Hampshire Agricultural Experiment Station as Scientific Contribution No. 645.

[2] Report of Massachusetts, New Hampshire, and Maine shellfish officials of September 26, 1972 meeting on Red Tide at Cat Cove Laboratory, Salem, Mass.

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is obvious that this dinoflagellate can grow under a wide range of temperatures and salinities. Prakash (1967) has shown that *G. tamarensis* achieves dominance in the surface waters of the Bay of Fundy at periods when the average temperature is 11.3 C and the average salinity is 31.9‰. Needler (1949) found a positive correlation between high temperature and high concentrations of *G. tamarensis* but Prakash's data do not confirm this observation. Prakash et al. (1971) credit salinity as being a more important environmental factor than temperature and in nonaxenic cultures of this organism they found optimal growth at salinities of 15–23‰ and reduced growth at higher salinities. Salinities of this low level are not even recorded in the 22-year averages from a baseline station where the organism occurs in abundance in the Bay of Fundy (Prakash 1967), indicating the difficulty of trying to extrapolate data obtained in culture to in-situ situations. The same culture experiments indicated that the organism required organic compounds, including humic acids (Prakash et al. 1971).

Cruises to collect coastal hydrographic data and information on phytoplankton populations from Rye, New Hampshire (43°8′N latitude, 70°41′W longitude) to Boston, Massachusetts (42°22′N 70°46′W) were conducted each month from August, 1971 to October 2, 1972. In addition, supplementary cruises were carried out in outer Boston Harbor in 1971 and 1972. The phytoplankton study was undertaken as part of Project NOMES[3], an evaluation of the biological consequences of dredging sand and gravel in Massachusetts Bay. Vertical and horizontal profiles were prepared from salinity and temperature data collected on these cruises (Table 1). The physical and chemical data provided a possible explanation for the initiation of the red tide bloom.

The surface temperature at Annisquam on August 7, 1972 was lower (11.9 C as compared with 14.3 C and 13.5 C for the Merrimack and Rye surface waters) even though the more southern stations are usually warmer. In addition, the surface salinity was higher at Annisquam (29.4‰) than it was at Merrimack (28.3‰) and Rye (28.5‰). Greater differences existed in August at the 5 and 10-m depths. The high-salinity, low-temperature characteristics of the surface water at Annisquam on August 7 indicate that a localized turnover of deep water had occurred. Similar upward movements of deep water in midsummer, 1966 and 1967, have

TABLE 1. Salinity and temperature records for four stations from Rye, N.H. to Bakers Island, Salem, Mass. obtained during the summer of 1972.

		July 12		Aug. 7		Sept. 17	
Salinity		Salinity (‰)	Temp. (*C*)	Salinity (‰)	Temp. (*C*)	Salinity (‰)	Temp. (*C*)
Rye, N.H.	Surface	27.5	12.9	28.5	13.5	29.4	15.0
	5 m	29.0	12.1	28.9	13.2	29.9	13.3
	10 m	29.3	10.5	29.4	10.9	30.0	11.2
	13 m	30.7	9.7	29.5	10.0	30.3	10.3
Merrimack River Newburyport, Mass.	Surface	25.8	16.8	28.3	14.3	27.1	15.8
	5 m	27.5	15.2	29.6	11.6	29.4	15.1
	10 m	30.2	10.3	29.7	8.5	29.7	14.9
	13 m	30.4	9.6	29.8[a]	8.3	29.8	14.7
Annisquam, Mass.	Surface	26.7	16.2	29.4	11.9	29.7	15.5
	5 m	28.4	13.5	31.2	9.8	29.7	14.7
	10 m	29.9	11.2	31.5	8.6	30.3	11.0
	11 m	30.1	10.9	–	–	30.3	11.0
Bakers Island, Salem, Mass.	Surface	25.5	18.0	29.2	16.1	29.4	16.2
	5 m	28.1	13.4	30.9	13.7	29.7	15.2
	10 m	30.2	10.1	29.7	9.4	29.8	12.9
	13 m	30.2	9.5	–	–	29.9	12.0

[a] At 12 m.

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[3] NOMES — New England Offshore Mining Environmental study NOAA040302211 and Sea Grant NG 30–72.

been demonstrated at Cape Nedick, Maine, (about 50 km north of Cape Ann) by Hulburt (1968). Graham (1970) showed that upwelling is the most prominent feature of the coastal circulation of the western Gulf of Maine.

The similarity between the salinities and temperatures at the Merrimack and Rye stations, together with the presence of a low-salinity cell of surface water (24.7‰) 1 mile to the north of the Merrimack station on September 17, suggests a northward movement of low-salinity surface water from the Merrimack River at that time.

Meteorological records from Logan Airport at Boston, Mass.[4] showed that prevailing winds in August 1972 were offshore. Offshore winds cause the surface coastal waters to move away from the shore enabling deeper water to move upward. Weather Bureau Records also show that the month of July had higher than usual rainfall, resulting in lower than normal salinities in the Cape Ann region. August 1972 was also noted as the driest August recorded at Boston since 1883. The period of dry weather produced stability in the water column. A heavy rainfall (3.15 inches in Boston) occurred on September 3, 1972 from Hurricane Carrie. This caused increased flushing and therefore movement of greater volumes of coastal water containing the *Gonyaulax* populations which had developed offshore into the estuaries where the populations of the soft-shelled clam (*Mya arenaria*) were located. The runoff water which is normally rich in inorganic and organic nutrients mixed with the ocean water. *Gonyaulax* populations developed to bloom proportions in the brackish nutrient-rich water of the estuaries.

Vertical and horizontal distributions of *G. tamarensis* were determined and are presented in Table 2. These data document the spread of the species to the north and show a gradual sinking of the population. The initial collection of *G. tamarensis* in our studies (5.1×10^3 cells/liter) was made from surface waters on July 29, 1972 at Graves Light in Boston Harbor. It was subsequently identified in surface waters at stations off Rye, Merrimack, Annisquam, Bakers Island, Flip Rock, and the Boston Light Ship.

The distribution of *G. tamarensis* was patchy; the surface waters appeared to be streaked. In

TABLE 2. Distribution of *Gonyaulax tamarensis* at stations from Rye, N.H. to Boston Harbor, Mass. during the summer of 1972.

Location	Date	Total No. of cells of *G. tamarensis* × 10^3/liter	No. of cysts of *G. tamarensis* × 10^3/liter
Rye surface	Sept. 17	119.8	1.3
5 m		12.7	
10 m		34.4	
15 m		15.3	
20 m (bottom)		15.3	
Merrimack surface	Aug. 7	2.5	
Merrimack surface	Sept. 17	70.0	33.1
5 m		79.0	
13 m (bottom)		100.7	10.2
Annisquam surface	Aug. 7	1.3	
Annisquam surface	Sept. 17	26.8	
5 m		73.8	
11 m (bottom)		132.5	
Bakers surface	Aug. 7	1.3	
Bakers surface	Sept.17	5.1	10.2
Boston Harbor (surface)			
Flip Rock	Aug. 7	2.5	
Flip Rock	Sept. 17	6.4	
Graves	July 29	5.1	
Graves	Sept. 9	1.3	
Graves	Sept. 17	1.3	
Boston Light Ship	Aug. 5	1.3	
Boston Light Ship	Sept. 9	5.1	
Minot's Light	Sept. 9	2.5	

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[4] Anon. 1972. Local Climatological Data, U.S. Department of Commerce, N.O.A.A., Boston, Mass., June–September.

samples collected from the reddest parts of streaks, there were 40 × 10^6 cells/liter in surface water at Annisquam on September 10 (C. Yentsch personal communication) and 2.8 × 10^6 cells/liter in surface water off the Isles of Shoals on September 15 (J. Sasner personal communication). The highest value recorded at our stations, where no attempt was made to sample streaks, was 133 × 10^3 cells/liter in bottom water at Annisquam on September 17.

The population of *G. tamarensis* was not distributed uniformly in the water column. At Annisquam on September 17, where the bloom originated in early September, the majority of the dinoflagellate population was at the greatest depth; whereas to the north at Rye, most of the dinoflagellates were present at the surface. In laboratory flasks, freshly collected water samples containing healthy populations of *G. tamarensis* showed a positive phototactic response. This indicates that on September 17, the bloom period had already occurred at Annisquam but was in progress at Rye.

A few cysts were present at the Rye and Annisquam stations, but on September 17, in surface waters at the Merrimack Station, nearly 50% of the cells of *G. tamarensis* were encysted. Since encystment of dinoflagellates is often a response to unfavorable environmental conditions (Prakash et al. 1971) and since a large proportion of the dinoflagellate population was in the lower portion of the water column, the conditions at Merrimack were assumed to be not conducive to the growth of *G. tamarensis* at that time.

Small populations (less than 6.4 × 10^3 cells/liter) of *G. tamarensis* were observed in our samples from Cape Ann south to Boston Harbor. This coincides with the near absence of paralytic shellfish poisoning from Massachusetts Bay. Although meteorological conditions were similar, hydrographic data collected in Massachusetts Bay in August indicated that no upwelling had occurred in this region. Upwellings, which are natural features of the waters of the Bay of Fundy (Gran and Braarud 1935) where paralytic shellfish poisoning commonly occurs (Prakash 1967), may be the primary causative factor for the development of large populations of *G. tamarensis*.

The vertical and horizontal distributions of *G. tamarensis* document the northward movement of the bloom and the sinking of the older population at Annisquam. The salinity and temperature profiles across the region of the red tide, obtained before the appearance of the bloom, have provided a potential explanation for the 1972 red tide in the Gulf of Maine.

It appears that three factors can be identified as responsible for the development of the *G. tamarensis* bloom: (1) the upwelling detected in the waters off Annisquam where the bloom appeared to be initiated; (2) the drier than normal weather in August allowed the resident population to utilize the upwelled water and greatly increase their numbers; and (3) the heavy rainfall associated with the September 3 hurricane can be conceived as the initiating event in moving the offshore population into the estuaries where they were ingested by the soft-shelled clams.

Acknowledgments — I am grateful to T. Norris, R. Beauregard, and F. deLara for assistance in collecting the field data and to C. Pinney for inverted microscope counts.

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Oxygen Consumption of Adult *Petromyzon marinus* in Relation to Body Weight and Temperature

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Beamish, F. W. H. 1973. Oxygen consumption of adult *Petromyzon marinus* in relation to body weight and temperature. J. Fish. Res. Board Can. 30: 1367–1370.

The logarithm of standard oxygen consumption of adult *Petromyzon marinus* increased linearly with the logarithm of weight at each of 5, 10, and 15 C. The proportionate change in standard oxygen consumption for a given change in temperature was independent of size, the mean regression coefficient being 0.949. Standard oxygen consumption for a sea lamprey of fixed weight increased from 52.7 to 124.0 mg/kg per hr over the range 5–20 C with the greatest changes occurring between 10–15 C, 64.5–114.3 mg/kg per hr. Active oxygen consumption was estimated for a few individuals at 10 C and found to be 475.5 mg/kg per hr, within the range reported for teleosts.

Beamish, F. W. H. 1973. Oxygen consumption of adult *Petromyzon marinus* in relation to body weight and temperature. J. Fish. Res. Board Can. 30: 1367–1370.

Le logarithme de la consommation standard d'oxygène chez *Petromyzon marinus* adulte augmente en relation linéaire avec le logarithme du poids à chacune des températures de 5, 10 et 15 C. Le changement de consommation standard d'oxygène correspondant à un changement donné de température est indépendant de la taille, le coefficient moyen de régression étant 0.949. La consommation standard d'oxygène chez une lamproie marine de poids constant augmente de 52.7 à 124.0 mg/kg/h dans les limites de 5 à 20 C, les plus grands changements se produisant entre 10 et 15 C, 64.5 et 114.3 mg/kg/h. Nous avons déterminé chez quelques individus la consommation d'oxygène pendant l'activité à 10 C et avons trouvé une valeur de 475.5 mg/kg/h, ce qui est dans les limites observées chez les téléostéens.

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Information on oxygen consumption of lampreys irrespective of species is scarce particularly for the adult phase (Randall 1970). In the present study, standard and to a lesser extent active oxygen consumption (Fry 1947) is considered in relation to temperature and size. While the linear relation between metabolism and weight has been demonstrated frequently for teleosts (Job 1955; Saunders 1963; Beamish 1964) it has seldom been demonstrated for lampreys, the experiments of Hill and Potter (1970) on ammocoetes of *Ichthyomyzon hubbsi* and Bourque (1970) on larvae of *Lampetra japonica* being notable exceptions.

Materials and methods — Sea lampreys in the final stages of metamorphosis (Beamish and Potter 1972) were collected during the autumn of 1970 and 1971 by electrofishing from Shelter Valley Creek, a tributary of Lake Ontario. Lampreys were transported to the laboratory where they were maintained in a sand substrate until assuming the predaceous feeding habits of adults.

Adult lampreys were maintained at 10 ± 1 C in 1200- and 2000-liter circular tanks supplied with aerated well water and exposed to a photoperiod of 16 hr. They were allowed to feed on white suckers, *Catostomus commersoni*, carp, *Cyprinus carpio*, and rainbow trout, *Salmo gairdneri*, for at least 2 months before being used for experimentation.

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Before sea lampreys were used in an experiment they were acclimated to a fixed temperature by a daily change of one degree and allowed at least 2 weeks at the desired temperature. Lampreys were deprived of food for 4 days before the start of an experiment to assure complete evacuation of the digestive tract (G. J. Farmer personal communication).

Oxygen content in the holding tanks was kept at 90–100% of air saturation irrespective of temperature and ammonia N generally was below 0.1 mg/liter.

Standard oxygen consumption was measured after the method employed by Smit (1965) and Claridge et al. (1973). A sea lamprey was placed in an acrylic tube and its spontaneous activity monitored by three photoelectric cells. Activity was recorded for 30 min during which the chamber remained sealed. During this period oxygen did not drop below 70% of air saturation. At the end of the closed period the chamber was flushed with fully aerated water. On introduction to the chamber most lampreys quickly attached to the inner surface and remained in this position, without registering activity counts, for most of the experimental period. Where this occurred the mean of the two lowest consumption rates was taken to represent the standard.

Lampreys were placed in respiration chambers approximately 16 hr before measurements were begun. Oxygen consumption was measured during the first 8 hr of the photoperiod to which lampreys were accustomed.

Results and discussion — The logarithm of standard oxygen consumption increased linearly with the logarithm of weight at 5, 10, and 15 C. The weight range of sea lampreys available at 20 C was not large enough to calculate a meaningful regression coefficient and the mean of the regressions for the lower temperatures was used to represent the rate of increase in oxygen consumption with weight. Thus the change in standard oxygen consumption with weight and temperature can be represented by the following equation:

Temp. (C)	Sample size	Weight (g)			
		Mean(Range)		*r*	SE of Estimate
5	20	22.8(5.2–95.0)	logY=–1.143+0.933 log X	0.813	0.282
10	17	34.8(6.8–100.0)	logY=–1.122+0.966 log X	0.840	0.215
15	19	35.7(9.0–139.8)	logY=–0.841+0.949 log X	0.889	0.167
20	9	75.6(36.0–137.7)	logY=–0.805+0.949 log X	–	–

where Y represents oxygen consumption as milligrams per hour and X the weight of sea lampreys in grams.

With the numbers of lampreys used at 5, 10, and 15 C, the small differences in regression coefficients in relation to their standard errors were such that it was not possible to demonstrate significant differences among slopes. Thus here as in investigations on teleosts (Wells 1935; Job 1955; Beamish 1964) the proportionate change in standard oxygen consumption for a given change in temperature appears to be independent of size.

The relation between oxygen consumption and body weight has not been established for the adult phase of other species of lampreys. However, for ammocoetes of *I. hubbsi* Hill and Potter (1970) found a logarithmic linear increase in oyxgen consumption with body weight the coefficient of which was 0.718. Bourque (1970) was unable to demonstrate a significant change in oxygen consumption per unit weight with increase in size of ammocoetes of *L. japonica*.

Among species of teleosts values for the regression coefficient have been reported from near surface proportionality to direct weight proportionality (Bertalanffy 1951; Sundnes 1957; Wohlschlog and Juliano 1959; Heusner et al. 1963; Beamish 1964, 1970).

To analyze the quantitative relation between temperature and standard oxygen consumption the value for a 100-g sea lamprey was calculated for each of the experimental temperatures from the equations above. Standard oxygen consumption at 5 C, 52.7 mg/kg per hr increased to 64.5 mg/kg per hr at 10 C before precipitously rising to 114.3 mg/kg per hr at 15 C and thereafter increasing only slightly to 124.0 mg/kg per hr at 20 C. Thus between 10–15 C, the Q_{10} was 3.1, approximately twice that between 5–10 or 15–20 C. Over the entire range of temperatures applied the Q_{10} was 1.8 which was about the same as the 1.6 found for adults of *Entosphenus tridentatus* between 5–15 C (Johansen et al. 1973). However, between 15–20 C the Q_{10} for *E. tridentatus* increased to 6.0. In contrast, Hill and Potter (1970) found the Q_{10} for ammocoetes of *I. hubbsi* to decrease with increasing temperatures but over the range 3.5–22.5 C exceeded 2.

Among adult lampreys oxygen consumption of *P. marinus* and *Lampetra fluviatilis* (Scherbakov 1937) were the same and 4.44 mg/hr when expressed for a 37-g individual at 15 C — the only weight and temperature for which a comparison can be made. Recently Johansen et al. (1973) measured oxygen consumption of nonfeeding *E. tridentatus* presumably captured on their upstream migration. For individuals of 250–350 g oxygen consumption was 30.3, 49.4, and 128.6 mg/kg per hr at 5, 15, and 20 C, respectively, compared with 49.0, 108.2, and 116.5 mg/kg per hr for *P. marinus* of similar weight at corresponding temperatures. The lower values recorded for *E. tridentatus* may reflect not only differences in metabolic rate among species but also the deterioration in physiological condition which accompanies sexual development during the upstream spawning migration. The metabolic rate of adult lampreys appears to be greater than that for ammocoetes (Randall 1973). Measurements of oxygen consumption for ammocoetes of *I. hubbsi* burrowed in a substrate of glass beads were made by Hill and Potter (1970) and presumed to represent standard or low routine rates. From their data an ammocoete of 5 g was estimated to consume 0.25 mg/hr at 15.5 C less than one half that consumed by an adult *P. marinus* of similar weight at 15 C. Oxygen consumption of ammocoetes of *L. japonica* sedentary in a substrate of plastic strands was estimated by Bourque (1970) to be 0.15 mg/hr at 10 C for individuals of 5 g. In contrast adults of *P. marinus* of the same weight are estimated to consume 0.36 mg/hr at 10 C. Leach (1946) measured oxygen consumption of large ammocoetes of *P. marinus* at 18 C and found rates higher than those estimated in this study for adults of similar size at 20 C. However, as suggested by Hill and Potter (1970) the values obtained by Leach were for free-swimming individuals and thus probably are well above the standard rate.

Active oxygen consumption was estimated for sea lampreys forced to swim in a respiration chamber as described by Farmer and Beamish (1969) with the exception that the portion in which lampreys were confined was lined with screening to prevens them from attaching to the inner surface. Most lampreys did not swim well for sufficient periodt to obtain a meaningful estimate of oxygen consumption. However, nine lampreys of mean weight 57.2 g (range 33.6–72.0) swam for periods of 20–60 min at velocities of 30–40 cm/sec at 10 C, the only temperature applied. Oxygen consumption for these individuals was 475.5 mg/kg per hr.

Among those teleosts for which information on their oxygen consumption is available, the salmonids provide a useful comparison with the sea lamprey in that they share similar thermal requirements (Smith 1972). Standard oxygen consumption of brook trout, *Salvelinus fontinalis*, at 10, 15, and 20 C was estimated as 79.3, 107.1, and 147.0 mg/kg per hr, respectively, for a 100-g fish (Beamish 1964) not appreciably different from the rates found for sea lampreys of similar size at corresponding temperatures. In accord, standard oxygen uptake of sockeye salmon, *Oncorhynchus nerka* (Brett 1964) and brown trout, *Salmo trutta* (Beamish 1964) are also of the same order as those found for sea lampreys under comparable conditions of weight and temperature. Active oxygen consumption of sockeye salmon of 50 g at 10 C was over 600 mg/kg per hr (Brett 1964) while that for wild rainbow trout of 79–398 g was 492 mg/kg per hr at 10 C (Dickson and Kramer 1971). For brook trout of 164 g active oxygen consumption was about 300 mg/kg per hr at 10 C (Basu 1959). Thus the active metabolic rate of adult sea lamprey is well within the range found for salmonids and indeed other teleosts (Basu 1959; Brett and Sutherland 1965; Beamish 1970). This is a little surprising in view of the relatively small gill area and tidal respiratory current in lampreys (Randall 1972). In adult *Lampetra planeri*, Sterba (1953) estimated the gill area as 1.5 cm^2/g less than the 1.5–12 cm^2/g reported for teleosts (Randall 1970). However, Johansen et al. (1973) found the ventilation–perfusion ratio, based on ventilatory volume and cardiac output, for *E. tridentatus* to be similar to values for teleosts and elasmobranches. Apparently a significant uptake of oxygen occurs across the skin of lampreys. Korolewa (1964) found up to 18% of the total oxygen consumption occurred across the skin of adult *L. fluviatilis*.

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Claw Loss and Other Wounds in Commercially Caught Lobsters (*Homarus americanus*)

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SCARRATT, D. J. 1973. Claw loss and other wounds in commercially caught lobsters (*Homarus americanus*). J. Fish. Res. Board Can. 30: 1370–1373.

Incidence of claw loss in commercially caught lobsters (*Homarus americanus*) ranged between 5 and 19% but could not be attributed to any single cause, although factors such as rough handling by fishermen, moving fishing gear, and ice in shallow waters may contribute. The incidence of other wounds ranged between 1 and 11% and there was evidence that serious wounding was related to the local practice of harvesting Irish moss by rakes.

SCARRATT, D. J. 1973. Claw loss and other wounds in commercially caught lobsters (*Homarus americanus*). J. Fish. Res. Board Can. 30: 1370–1373.

Il y a perte des pinces dans 5–19% des cas chez les homards (*Homarus americanus*) capturés commercialement, mais on ne peut attribuer ces pertes à un facteur en particulier, bien que la manutention peu soignée par les pêcheurs, les engins de pêche mobiles et la glace en eau peu profonde peuvent tous y contribuer. On observe d'autres blessures chez 1–11% des individus, et il y a des indications que la pratique courante de récolte de la mousse d'Irlande au râteau est responsable de blessures sérieuses.

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ALTHOUGH lobsters normally have two chelae, a few may always be found which have lost one or both claws or have been unjured in some other way. Such lobsters weigh less and may be worth less per unit weight than intact lobsters. Claw loss may be caused by stress, such as inter- and intraspecific competition, rough handling by fishermen, and fishing gear moving across the sea bed. The incidence and prevention of claw loss and wounding are of considerable interest to commercial fishermen.

Following adoption of drag raking for Irish moss (*Chondrus crispus*) in the summer of 1969 in the North Rustico area of Prince Edward Island (Fig. 1), commercial fishermen complained of an increase in the number of wounded lobsters, including those missing one or both claws, in their catches the next lobster fishing season, May–June 1970. They attributed this increase to the raking. Underwater observations showed that lobsters were being wounded by rakes and boulders disturbed by rakes (Scarratt 1972, 1973). Raking was particularly heavy in the summer of 1970.

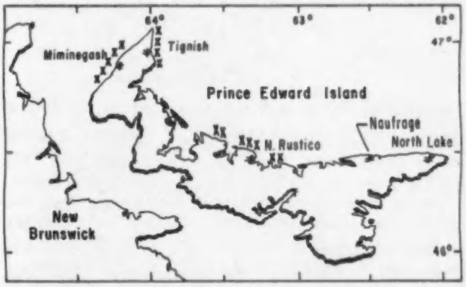

FIG. 1. Location of study ports in Prince Edward Island. Areas of Irish moss raking are marked XXX. The moss beds near North Rustico were raked in 1969 and 1970 only.

During the spring lobster fishing season of 1971, commercial catches were examined at North Rustico and Tignish where moss had been raked to see what damage was detectable, and at North Lake and Naufrage where no raking occurs but where storm-tossed moss is harvested off the beach (Ffrench 1971). The 1971 summer season (August–October) lobster catches were examined at Miminegash where moss is also raked.

In 1971, a ban on moss raking was imposed in the North Rustico area, commencing immediately after the close of the spring lobster season in June. Thus, there was no raking during the 1971 lobster-growth period or before the 1972 fishing season when catches were examined again.

This paper presents results of these catch examinations, compares them with records from other ports, and discusses causes of the damage observed.

Methods — Observers accompanied commercial lobster fishermen at each of the ports, and examined all lobsters taken from the traps. Each lobster was measured (carapace length (C.L.) in mm), examined for claw loss or regeneration and other injuries, and the sex recorded. Injuries were assigned to one of three categories based on their superficial appearance. These were: *light* – with minor cuts and cracks, including loss of claw tips; *moderate* – with minor crushing; and *severe* — with major crushing or excision of tissues. Wounds caused during handling were noted. Sublegal and berried lobsters were subsequently returned to the sea. With the exception that these illegal lobsters were temporarily retained on board, there were no detectable differences in handling lobsters compared with normal fishing practice and no reason to assume a changed damage rate.

Naufrage and North Lake catches were from moderately deep water; Tignish and Miminegash catches were from shallow water. (Miminegash records are incomplete in that only claw loss was recorded fully and details of wounds are not known.) Catches from North Rustico in 1971 were from deep water in the early part of the season and from shallow water in the

TABLE 1. Numbers of lobsters missing one or both claws at study ports in P.E.I.

Year	Port	Fishing depth (*m*)	Raking for Irish moss	Total lobsters examined	Lobsters missing 1 claw	Lobsters missing 2 claws	Total lobsters missing claws (%)
1971	Naufrage	15–20	None	1543	106	7	7.4
	North Lake	12–18	None	381	15	2	4.4
	Tignish	7–15	Annual	2347	106	4	4.7
	Miminegash	2–10	Annual	1890	69	6	4.0
	North Rustico	15–20	None	1815	110	3	6.3
	North Rustico	2–8	1969–70	7204	942	44	13.7
1972	North Rustico	4–18	1969–70	3370	591	48	19.0

later part. This is normal commercial practice in this area. Fishing begins in deep water and moves inshore as the season progresses. Fishermen believe lobsters move inshore as the water warms up. In 1972 catches were examined from shallow water at North Rustico only.

Results and Discussion — Numbers of lobsters missing or regenerating one or both claws — Fishermen's catches were observed on 23 days and a total of 18,567 lobsters examined.

There were no significant differences in frequency of occurrence of lobsters missing or regenerating claws between deep water catches at North Rustico, Naufrage, and North Lake (Table 1) ($\chi^2 = 4.54$, df = 2, $P > .1$). Incidence of claw loss did not exceed 7.4%.

At Tignish and Miminegash, where moss beds are smooth and lobster populations on them are relatively low, claw loss was about 4%. By contrast at North Rustico in shallow water, where moss beds are rough and the lobster populations on them are high (Scarratt 1972, 1973), claw loss was 13.7%. This was significantly higher than the North Rustico deep-water sample ($Z = 14.3$, $P < .001$) and indicated the presence in shallow water of some factors which caused a high rate of claw loss.

The assumption in the spring of 1971 was that moss raking had caused this higher claw loss; however, in 1971, following the close of the lobster season, moss raking was banned. This ban therefore eliminated that cause of claw loss or injury and lobsters might then be expected to have ample opportunity to regenerate claws during the 1971 growing season. Yet catches in 1972 showed an increase rather than a reduction in the number of clawless lobsters (Table 1) ($Z = 13.8$, $P < .001$), suggesting causes other than moss raking. This could be due to aggressive interactions amongst individuals in a relatively highly populated area. The principal cause in this area, other than rough handling of sublegal lobsters by fishermen, seems most likely to be winter ice which piles up on the Prince Edward Island shores in depths out to 6–8 m. In the winter of 1972, ice was unusually severe and persisted unusually late. Conceivably, ice scouring or resting on bottom could damage lobsters burrowed under stones.

Examination of lobster catches elsewhere (D. G. Wilder personal communication) gave the following percentages of legal-sized lobsters missing one or both claws:

Date	Location	Lobsters examined	% missing claws
1965	Pictou, N.S.	23,700[1]	4.7
1965	Miminegash, N.S.	12,458	5.5
1965–66	Yarmouth, N.S.	2009	7.2
1966	Yarmouth, N.S.	2886	9.7
1966–67	Port Maitland, N.S.	1960	7.8
1968–69	Port Maitland, N.S.	3812	12.0
1972	Continental slope (Georges Bank to Baccaro Bank)	495	9.9

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[1] Estimated.

Considering these and the Prince Edward Island figures, the normal frequency of lobsters missing one or both claws ranges from less than 5 to 19% and appears to be governed by no single factor. It seems reasonable to assume that claw loss and physical stress are related, yet areas where fishermen normally handle lobsters roughly, e. g. Tignish and Miminegash, may have low incidence of claw loss, and areas where traditionally fishermen have been careful may have high incidence. There are clearly more factors governing this than have been elucidated in this study.

TABLE 2. Percentage of lobsters bearing wounds and the percentage of wounds in different classes of severity. The number of lobsters examined is given in Table 1.

		Percentage of lobsters with wounds to:					Severity of wounds (%)		
Year	Port	claws	carapace	abdomen	tail fan	Total	light	moderate	severe
1971	Naufrage	3.8	5.3	1.0	1.0	11.1	88.4	8.1	3.5
	North Lake	2.6	0.3	0.0	0.0	2.9	72.0	28.0	0.0
	Tignish	4.1	0.3	0.1	0.8	5.3	32.3	45.7	30.0
	Miminegash			Not known		1.1		Not known	
	North Rustico (deep)	4.8	1.8	0.5	1.4	8.5	59.8	21.7	18.8
	North Rustico (shallow)	4.6	2.1	0.7	0.3	7.6	70.7	18.6	10.7
1972	North Rustico	3.3	0.1	0.0	0.5	3.9	69.7	20.5	9.8

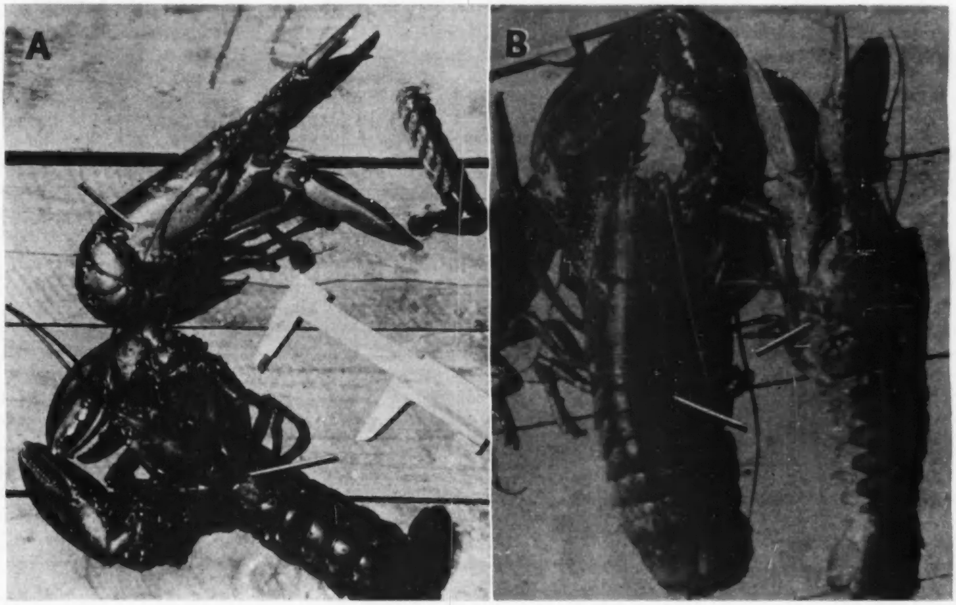

FIG. 2. Wounded lobsters taken in commercial catches June 1971, North Rustico. A, *Upper*: posterior margin of carapace broken away exposing gills. *Lower*: extensive cracking and depression of carapace in cardiac region; B, *Left*: wounding of abdomen, right antero-lateral segments. *Right*: deep incision of left side of carapace exposing and involving gills and bases of walking legs.

Scarratt — J. Fish. Res. Board Can.

TABLE 3. Number of lobsters examined at study ports, in three size groups, the percentage missing or regenerating claws and bearing other wounds.

		Shorts C.L. <63.5 mm			Canners C.L. 63.5–80.9 mm			Markets C.L. >81.0 mm		
Year	Port	Total examined	Missing claws (%)	Wounded (%)	Total examined	Missing claws (%)	Wounded (%)	Total examined	Missing claws (%)	Wounded (%)
1971	Naufrage	648	6.6	9.7	870	7.8	10.7	25	2.0	8.0
	North Lake	221	4.5	1.4	7	5.0	3.6	20	0	1.0
	Tignish	1089	4.6	5.1	1205	4.8	4.3	53	3.8	5.7
	Miminegash	1399	3.0	0.9	455	7.0	1.5	36	0	0
	North Rustico (deep)	764	5.8	7.5	968	6.8	8.2	74	2.7	1.4
	North Rustico (shallow)	5470	13.7	6.8	217	14.2	5.6	151	10.6	5.3
1972	North Rustico	2753	18.4	3.9	544	24.3	5.0	52	11.5	0

There was no relation between claw loss and lobster size (Table 3).

Numbers of lobsters with other wounds — With the exception of lobsters examined at Naufrage, most wounds were located on the claws and nearly all were light, consisting of simple cracks or loss of claw tips (Table 2).

At Naufrage, due to the handling system used aboard the boat in question, a large number of wounds were broken rostra which considerably increased the number in "wounds to carapace."

The number of wounds on carapace or tail region is not generally any higher in areas where raking takes place although the incidence of serious wounds is higher (Table 2). In particular, wounds involving heavy cutting or crushing of carapace and abdomen (Fig. 2) were seen only at North Rustico and Tignish. These wounds were comparable in all respects with wounds seen by divers to be caused by moss rakes in operation. They were larger and deeper than those seen to be caused by claws of other lobsters in traps or on fishing boats. There were no significant differences in frequency of wounding between sublegal and commercial lobsters (Table 3).

Even at North Rustico and Tignish the numbers of lobsters with these deep or serious wounds were not very high. For example, in shallow water at North Rustico in 1971, 7204 lobsters were examined of which 59 carried severe wounds. Nevertheless this represents, on average, 10 severely wounded lobsters seen aboard each lobster boat each day. In deeper water, earlier in the season, the numbers were slightly higher, about 15 per boat per day. This indicates fairly clearly some lobster movement between shallow water and deeper water, possibly related to the seasons.

Conclusions — Clearly, the incidence of claw loss cannot be attributed to any single cause, and for that reason, cannot be used as evidence of stress from any particular source. It is quite conceivable that high incidence of claw loss at North Rustico in 1971 was due to moss raking during the previous summer. However, the even higher incidence in 1972 cannot be attributed to raking, and could possibly have been caused by ice.

The high incidence of severe wounds, particularly those involving deep crushing, does appear to be related to a past history of moss raking, although it is clear that this is only an indication of stress on the population, and cannot be used to estimate total impact. More important though, it is easy to understand how lobster fishermen, not familiar with this type of wounding on lobsters, would become alarmed if something like 1% of their catch suddenly began to show evidence of deleterious effects of another competing fishery.

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Intertidal Feeding of Winter Flounders (*Pseudopleuronectes americanus*) in the Bay of Fundy[1]

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WELLS, B., D. H. STEELE, AND A. V. TYLER. 1973. Intertidal feeding of winter flounders (*Pseudopleuronectes americanus*) in the Bay of Fundy. J. Fish. Res. Board Can. 30: 1374–1378.

Flounders captured in summer in the intertidal zone at high tide fed mainly on food species that live in that zone. Flounders captured in the subtidal zone fed partially on food species that live there, and partially on intertidal food species. From these feeding habits, and from the magnitude of the movement into the intertidal zone (previously reported), we conclude that large intertidal areas are major feeding grounds for winter flounder. The quantities of filamentous algae in the stomachs suggest that winter flounders can utilize plant material.

WELLS, B., D. H. STEELE, AND A. V. TYLER. 1973. Intertidal feeding of winter flounders (*Pseudopleuronectes americanus*) in the Bay of Fundy. J. Fish. Res. Board Can. 30: 1374–1378.

Des plies rouges capturées en été, à marée haute, dans la zone intertidale avaient mangé surtout des organismes habitant cette zone. Les plies capturées dans la zone sublittorale contenaient en partie des organismes de cette zone, en partie des organismes de la zone intertidale. Nous basant sur ses habitudes alimentaires et sur l'amplitude du mouvement de pénétration de la plie dans la zone intertidale (mentionnée dans une publication antérieure), nous concluons que de grandes superficies intertidales sont des aires d'alimentation importantes de cette espèce. A en juger par les quantités d'algues filamenteuses trouvées dans les estomacs, la plie rouge peut utiliser le matériel végétal.

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THIS report presents evidence from stomach contents that the intertidal zone in the Bay of Fundy is a major summer feeding ground for winter flounder, *Pseudopleuronectes americanus*. In other areas, intertidal waters are too warm to allow this (McCracken 1963). Large scale movement of winter flounder into such areas begins shortly after low tide. The fish occupy the zone for almost 7 hr and then leave with the falling tide in the 3-hr interval before low tide (Tyler 1971).

We compared the major foods of the fish that occupied the intertidal zone with foods of those that remained in the subtidal zone at high tide to investigate whether or not food differences between the two groups of fish were related to distribution of the prey in the respective zones.

Methods — Following high tide, 43 flounders (23–43 cm) were speared by SCUBA divers in the intertidal zone, and 41 (22–42 cm) in the subtidal zone of Brandy Cove, Passamaquoddy Bay, N.B. (Part of Bay of Fundy). The length-frequency distribution for each sample was similar to the distribution previously published for Brandy Cove (Tyler 1971), except that flounders less than 20 cm were not taken. Upon capture their spinal cords were severed, the abdominal walls slit, and the bodies immersed in 20% formalin/sea water solution. Later, the digestive tracts were removed, tied off, and preserved in 80% ethyl alcohol. Prey species were identified, counted, and weighed to the nearest .01 g. This report compares those major food items that comprised 70% of the weight of the stomach contents.

Infauna of the intertidal and subtidal zones was sampled by hand using a 0.0225 m^2 Ekman grab at 6-m intervals along a 120-m line transect at right angles to the shoreline. Eleven samples were intertidal and 10 subtidal. Intertidal samples were collected at low water and subtidal ones by SCUBA divers. All depths were estimated by SCUBA depth gauge and corrected to depths at mean high water. Where the nature of the bottom prevented efficient operation of the grab, the corners were pegged and the sample dug with a small shovel. The sediments were washed through a series of standard, graduated wire sieves with mesh sizes of 0.5, 1.0, 4.0, and 8.0 mm. After washing, sub-sieve particles and the smallest sieves were placed

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TABLE 1. Stomach contents of the winter flounder from the intertidal zone. Asterisk indicates weights less than 0.10 g.

Species name	Total wet wt in all stomachs (*g*)	% by weight	% stomachs with item	No. of prey individuals
Acrosiphonia arcta	36.03	20.0	27.9	–
Peloscolex benedeni	24.05	13.2	27.9	–
Gammarus oceanicus	23.64	13.0	46.5	479
Enteromorpha intestinalis	23.27	12.8	48.8	–
Cladophora sericea	13.43	7.4	11.6	–
Nereis virens	8.56	4.7	18.6	8
Gammarus lawrencianus	6.02	3.3	20.9	426
Pilayella littoralis	5.97	3.3	16.3	–
Amphithoë rubricata	5.74	3.1	44.2	155
Ectocarpus siliculosus	5.00	2.7	7.0	–
Mya arenaria	4.15	2.3	27.9	51
Polydora sp.	3.85	2.1	4.7	10
Littorina littorea	3.26	1.8	7.0	38
Acmaea testudinalis	2.61	1.4	4.7	11
Nephtys incisa	1.98	1.1	18.6	17
Cricotopus sp.	1.68	.9	79.1	809
Ulva lactuca	1.23	.6	7.0	–
Clymenella torquata	1.03	.5	14.7	33
Harmothoe imbricata	.98	.5	7.0	6
Nemertea	.63	.3	7.0	7
Glycera americana	.55	.3	2.3	1
Edotea montosa	.45	.2	11.6	31
Mytilus edulis	.42	.2	25.6	56
Photidae	.41	.2	18.6	3
Ammotrypane aulogaster	.34	.1	7.0	8
Pholis gunnellus	.24	.1	2.3	1
Jaera albifrons	.19	.1	9.3	13
Leptocheirus pinguis	.19	.1	9.3	11
Eteone longa	.19	.1	16.3	85
Crangon septemspinosa	.18	.1	2.3	1
Chiridotea caeca	.15	.1	2.3	2
Amphipoda	.11	.1	7.0	3
Cistenides gouldii	*	*	2.3	1
Eulalia sp.	*	*	2.3	1
Tharyx acuta	*	*	2.3	26
Rhodymenia palmota	*	*	7.0	–
Pygospio elegans	*	*	25.6	15
Scoloplos armiger	*	*	4.7	4
Nucula proxima	*	*	2.3	1
Corophium volutator	*	*	2.3	7
Phoxocephalus holbolli	*	*	4.7	2
Hydrobia minuta	*	*	7.0	6
Micrura sp.	*	*	2.3	2
Nematoda	*	*	7.0	4
Lunatia heros	*	*	4.7	3
Fucus vesiculosus	*	*	2.3	–
Polychaeta	*	*	2.3	4
Macoma balthica	*	*	2.3	2
Copepoda	*	*	4.7	7
Neptunea decemcostata	*	*	2.3	1
Dexamine spinosa	*	*	2.3	1
Praxillella praetermissa	*	*	2.3	1
Lumbrineris fragilis	*	*	2.3	1
Nainereis sp.	*	*	2.3	1
Debris	4.90	2.69	25.6	–

TABLE 2. Stomach contents of the winter flounder from the subtidal zone. Asterisk indicates weights less than 0.10 g.

Species name	Total wet wt in all stomachs (*g*)	% by weight	% stomachs with item	No. of prey individuals
Pilayella littoralis	37.38	22.4	19.5	–
Leptocheirus pinguis	31.44	18.8	53.7	1439
Enteromorpha intestinalis	23.90	14.3	26.8	–
Peloscolex benedeni	14.89	8.9	4.9	–
Mya arenaria	10.42	6.2	29.3	77
Lumbrineris fragilis	6.99	4.2	14.6	8
Cladophora sp.	5.32	3.2	9.8	–
Gammarus lawrencianus	3.81	2.3	7.3	198
Nereis virens	2.67	1.6	7.3	4
Harmothoe imbricata	1.74	1.0	19.5	10
Amphithoë rubricata	1.14	.6	7.3	18
Acrosiphonia arcta	1.12	.6	2.4	–
Edotea montosa	1.10	.6	14.6	49
Gammarus oceanicus	.85	.5	16.8	31
Cerastoderma pinnatulum	.72	.4	22.0	15
Cistenides gouldii	.70	.4	22.0	13
Cricotopus sp.	.65	.3	12.2	40
Ammotrypane aulogaster	.52	.3	19.5	19
Didemnum candidum	.41	.2	2.4	2
Nucula proxima	.31	.1	4.9	2
Balanus balanoides	.24	.1	2.4	2
Ischnochiton ruber	.24	.1	4.9	3
Yoldia (*sapotilla* ?)	.15	.1	4.9	2
Nephtys incisa	.14	.1	2.4	1
Casco bigelowi	.13	.1	4.9	4
Nereidae	*	*	2.4	1
Nucula tenuis	*	*	4.9	1
Ninoe nigripes	*	*	2.4	1
Solemya borealis	*	*	2.4	1
Cucumaria frondosa	*	*	2.4	1
Aphroditoidea	*	*	4.9	1
Nematoda	*	*	7.3	29
Cirratulus cirratus	*	*	2.4	1
Young *Macoma*	*	*	2.4	4
Macoma balthica	*	*	2.4	1
Terebelloides stroemi	*	*	4.9	2
Littorina saxatilis	*	*	2.4	5
Littorina littorea	*	*	2.4	2
Thais lapillus	*	*	2.4	1
Mytilus edulis	*	*	4.9	9
Nemertea	*	*	12.2	2
Syllis gracilis	*	*	7.3	3
Phoxocephalus holbolli	*	*	2.4	2
Unciola irroratus	*	*	2.4	2
Maldanidae	*	*	2.4	1
Strongylocentrotus drōebachiensis	*	*	2.4	1
Hydrobia minuta	*	*	4.9	4
Polynoidae	*	*	2.4	1
Scoloplos armiger	*	*	2.4	1
Eudorella truncata	*	*	2.4	1
Polydora sp.	*	*	2.4	1
Spirorbis borealis	*	*	2.4	2
Praxillella gracilis	*	*	2.4	1
Debris	17.17	10.28	26.8	–

TABLE 3. Numbers of individuals of principal food-species taken in sediment samples on the transect. Asterisk indicates numbers of individuals of algae could not be determined.

	Sample depth at mean high tide (*m*)																				
	Intertidal											Subtidal									
Species	4.3	4.9	5.2	5.5	5.5	5.5	5.5	5.8	5.8	5.8	6.4	6.4	6.7	6.7	7.0	7.3	7.3	7.6	7.9	8.2	8.5
Enteromorpha intestinalis	.	.	*	.	*	*	*	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Acrosiphonia arcta	*	*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cladophora sericea	.	.	*	.	.	*	.	.	*	*	*	.	.	.	*	*	.	.	.	.	.
Gammarus oceanicus	78	19	108	34	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Peloscolex benedeni	.	.	.	.	1	2	.	8	5	16	4	.	.	.	.	.	.	.	.	.	.
Nereis virens	5	1	6	6	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Mya arenaria	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	3	.
Leptocheirus pinguis	.	.	.	.	.	.	.	.	.	.	.	3	.	.	2	3	4	10	1	1	3
Lumbrineris fragilis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.

in anesthetic solution in a white enamel pan so that certain organisms would loosen their holds on the screens. Organisms were then identified, counted, and weighed.

Results and discussion — Six species made up 70% of the total weight of food in all stomachs of the intertidal zone fish (Table 1). Three of the six species were algae: *Acrosiphonia arcta*, *Enteromorpha intestinalis*, and *Cladophora sericea*. Together these species made up 40% of the weight of the combined stomach contents. *Gammarus oceanicus* comprised 13.0%, and the oligochaete, *Peloscolex benedeni*, 13.2%. Also important were *Nereis virens*, *Gammarus lawrencianus*, *Pilayella* (= *Pylaiella*) *littoralis*, and *Amphithoë rubricata*, with values of 7.4%, 3.3%, 3.3%, and 3.1%, respectively. Seventy-nine percent of the stomachs contained chironomid larvae, *Cricotopus* sp., which were entangled in clumps of *Acrosiphonia* and *Enteromorpha*.

Five species made up 70% of the total weight of food in all stomachs of the subtidal fish: *Pilayella littoralis*, *Leptocheirus pinguis*, *Enteromorpha intestinalis*, *Peloscolex benedeni*, and *Mya arenaria* (Table 2). Three species of algae, *Pilayella littoralis*, *Enteromorpha intestinalis*, and *Cladophora* sp. made up 40% of the food. *Peloscolex benedeni* comprised 8.9%. The amphipod, *Leptocheirus pinguis*, was an important prey comprising 18.8% of the weight. This species occurred as only 0.11% of the weight in the intertidal stomachs. The clam, *Mya arenaria*, made up 6.2% of the weight, as opposed to 2.3% in the intertidal sample. The polychaete, *Lumbrineris fragilis*, made up 4.2% of the subtidal sample, but was negligible in the intertidal sample.

Intertidal and subtidal fish were similar in that both ate filamentous algae and both took *Peloscolex* as an important prey. The transect data show that these species are found mainly in the intertidal zone (Table 3). Only the intertidal group took *Gammarus oceanicus* as an important prey. This species was found exclusively in the intertidal portion of the transect. *Lumbrineris and Leptocheirus* were important to subtidal, fish only. These species were found in the subtidal, but not in the intertidal samples. *Mya* was found in both intertidal and subtidal areas, but appeared somewhat more important to subtidal fish. Distributional information would have been strengthened by more substrate samples, but the zonal relations are clear from the data.

Intertidal food species are important to fish caught in the intertidal and subtidal zones. Large scale movement of winter flounders into the intertidal zone has been reported (Tyler 1971). On the basis of these facts we conclude that the area is a major feeding ground. Because of the value of large intertidal flats and beaches to winter flounder production, such acreage should be protected from destructive human intervention.

Since as much as 40% of the weight of stomach contents was algae, we suspect that flounders are functional omnivores. A similar conclusion was also reached by Thomas (1970) who found that flounders in the Bideford Estuary, Prince Edward Island, had six times more filamentous algae by weight than any other food item. At Newfoundland locations, 13–19% of the total weight of stomach contents of winter flounder was "plant material" (Kennedy and Steele 1971). It is possible that the fish swallowed the algae while feeding on the chironomids living in it, and that the algae are nutritionally useless. This interpretation seems unlikely because of the quantities of algae consumed. Laboratory experiments, to determine the growth-ration relations for flounders fed on filamentous algae, would clarify the problem. If it proves true that a marketable, northern marine fish assimilates plant material, it could be highly significant for aquaculture, and interesting from a natural productivity standpoint, since primary production is converted directly to fish flesh. Previously, northern marine fishes were considered strictly carnivorous.

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First Records of the Silver Shiner, *Notropis photogenis*, from Canada

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Gruchy, C. G., R. H. Bowen, and I. M. Gruchy. 1973. First records of the silver shiner, *Notropis photogenis*, from Canada. J. Fish. Res. Board Can. 30: 1379–1382.

A series of specimens of the silver shiner, *Notropis photogenis*, from the Grand River drainage of Ontario provide the first records for the species from Canada. The specimens are described and some aspects of their ecology are discussed. The species is believed to be indigenous to Canada.

Gruchy, C. G., R. H. Bowen, and I. M. Gruchy. 1973. First records of the silver shiner, *Notropis photogenis*, from Canada. J. Fish. Res. Board Can. 30: 1379–1382.

La capture d'une série de spécimens du méné argenté, *Notropis photogenis*, dans le bassin ontarien de la Grande rivière permet de signaler pour la première fois la présence de cette espèce au Canada. Nous décrivons les spécimens et examinons certains aspects de leur écologie. On croit que l'espèce est indigène au Canada.

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Until now, the range of *Notropis photogenis*, the silver shiner, has been considered to be restricted to the United States. It is known from north central Indiana and southeastern Michigan to western New York and southward to Tennessee and North Carolina (Hubbs and Lagler 1958; Trautman 1957). The silver shiner is a fluviatile species, found primarily in large clear streams (Trautman 1957). We have found specimens of silver shiners in collections recently made in southwestern Ontario. This species, which has not previously been recorded from Canada (Scott and Crossman 1969), is, overall, similar to the rosyface shiner, *Notropis rubellus*, and the emerald shiner, *Notropis atherinoides*.

In this paper, we describe the Ontario specimens of silver shiner and point out characteristics to identify them positively, especially with respect to rosyface and emerald shiners. Data are included on some aspects of the ecology of the silver shiner. We discuss the recent appearance of the silver shiner in Canadian waters and include a key to separate *N. photogenis* from similar congeners.

Materials and methods — From July 29 to August 8, 1971, R. H. Bowen made 35 collections of fishes in the Grand River drainage, Ontario. Among these collections, which are now catalogued in the National Museum of Natural Sciences, four were found to contain specimens of *N. photogenis*: NMC71–850, Grand River, Lorne Park, Brantford (43°08′N, 80°16′W), 2 specimens; NMC71–854, Grand River at the mouth of Schneider Creek near Doon (43°24.5′N, 80°25′W), 11 specimens; NMC71–855, Grand River 100 m upstream from the mouth of Schneider Creek (43°24.5′N, 80°25′W), 8 specimens; NMC71–857, Conestogo River near St. Jacobs (43°32.5′N, 80°34.5′W), 18 specimens. The specimens ranged in size from 32.5 to 108 mm in standard length, and among 14 of the larger specimens there were eight males and six females. Ichthyologists from the Royal Ontario Museum subsequently collected 12 specimens of silver shiner from Lorne Park, Brantford, and a location near Paris, Ontario (ROM Acc. No. 1945). These specimens were made available for this study. For the present paper, we have examined a total of 47 silver shiners (listed above), 31 emerald shiners, and 35 rosyface shiners; the latter two species are from several collection sites in southwestern Ontario. Our identification of *N. photogenis* has been confirmed by Dr R. M. Bailey, Museum of Zoology, University of Michigan.

We have generally followed Hubbs and Lagler (1958) in describing features for the characterization of *N. photogenis*, but some measurements used by us are not defined by them. These latter are as follows: dorsal–caudal length, from the origin of the dorsal fin to the caudal flexure; eye–dorsal, from the posterior margin of the orbit to the origin of the dorsal fin; pelvic–caudal length, from the origin of the pelvic fin to the caudal flexure. Placement of scales at the origin of the dorsal fin was found to be irregular, therefore scale rows above the lateral line were counted on the diagonal row starting beneath the second dorsal ray. Vertebral centra were counted from X-rays and include the four centra of the Weberian apparatus.

Identification — Among Cyprinidae now known to occur in Canada, *N. photogenis* is likely to be confused only with the rosyface shiner or the emerald shiner. On the basis of characteristics in the key by Scott and Crossman (1969), *N. photogenis* would probably be determined as *N. rubellus* as it has a long "sharp" snout and the lateral pigmentation extends below the lateral line. All three species, however, are substantially different in several characteristics. The mid-dorsal stripe in *N. photogenis* is narrower and more clearly distinguished from the general dorsal pigmentation than is the case in either *N. rubellus* or *N. atherinoides* (Fig. 1). Futhermore, as can be seen in Fig. 1, the overall dorsal pigmentation is much more dense in *N. rubellus* than in *N. photogenis*. Medial to the nostrils in *N. photogenis* a pair of distinct crescent-shaped patches are usually visible (Fig. 2); these do not occur in *N. rubellus* or *N. atherinoides*. These patches are not always apparent, especially in preserved material, but when obvious, are characteristic of *N. photogenis* (Trautman 1957). In silver shiners the origin of the dorsal fin is directly above the insertion of the pelvic fin, while in the rosyface and emerald shiners the dorsal origin is distinctly posterior to the pelvic insertion (Fig. 3).

Some morphometric measurements will separate both adults and juveniles of silver shiners from rosyface and emerald shiners, but others may separate specimens at only one stage of maturity of one of the species. The ratio of dorsal–caudal length to pelvic–caudal length in both adult and juvenile *N. photogenis* is equal to or greater than 0.91 while in *N. rubellus* and *N. atherinoides* it is equal to or less than 0.91 (Table 1). Similarly, the ratio of eye–dorsal to dorsal–caudal is equal to or less than 1.0 throughout the range in size in our sample

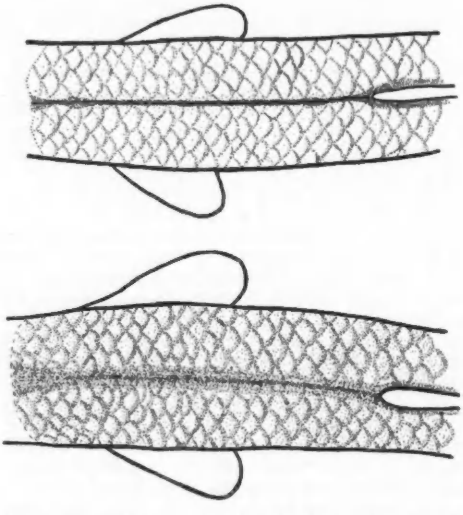

FIG. 1. Dorsal view of *Notropis photogenis* (above), showing narrow, well-defined mid-dorsal strip and light dorsal pigmentation, and dorsal view of *N. rubellus* (below), showing the wide, diffuse mid-dorsal stripe and dense dorsal pigmentation.

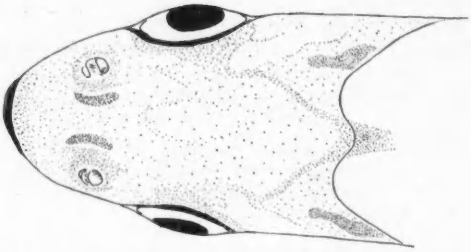

FIG. 2. Dorsal view of the head of *N. photogenis*, showing the crescent-shaped patches of pigmentation medial to the nostrils.

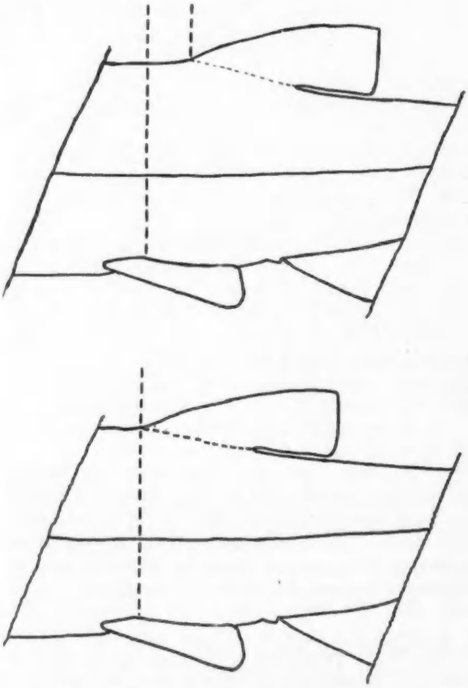

FIG. 3. The relative position of the origin of the dorsal fin and the insertion of the ventral fin in *N. rubellus* and/or *N. atherinoides* (above) and *N. photogenis* (below).

of *N. photogenis*, but in both *N. rubellus* and *N. atherinoides* it is greater than 1.0 (Table 1). On the other hand, the ratio of snout length to orbit diameter will distinguish only adults of emerald shiners from adults of rosyface and silver shiners (Table 1).

We have found that several meristic characters (in combination) will distinguish the three above-mentioned species. In the sample studied, there were five scale rows above the lateral line in *N. photogenis*, five or six in *N. rubellus*, and six in *N. atherinoides*. Silver and emerald shiners typically had 15 or 16 pectoral rays (exceptionally 17) but there were 12 or 13 (exceptionally 11 or 14) in rosyface shiners. Numbers of vertebral centra or pharyngeal teeth were not sufficiently distinctive in any of the three species to be of use in distinguishing them (Table 1). Additional meristic data on the Ontario specimens of *N. photogenis* are given in Table 1; they fall within the ranges given in the literature for the species.

Ecology — Each of the four localities where silver shiners were found had muddy or cloudy water between 75 and 100 cm in depth. There was medium to fast current at each locality, and the habitats may be described as deep riffles of flowing pools with gravelly to stony bottoms which had only light silt deposits. There was some submergent vegetation (unidentified) at each site. At three of the collection sites the river width exceeded 20 m, but at Lorne Park, Brantford, the collection site was only 5 m wide. Water temperatures ranged from 19 to 23 C at the various collection sites. This habitat is not significantly different from that described by Trautman (1957) for *N. photogenis* in Ohio, except that he noted that silver shiners preferred clear streams.

Apparently Trautman (1957) is the only authority who has commented on the feeding habits of the silver shiner, and he mentioned merely that they may jump for flying insects. We examined the stomach contents of nine large specimens of silver shiner, and found Trichoptera larvae in three individuals, the eyes of adult Diptera in two, small adult Coleoptera in two, and two small turbellarians in one. These stomach contents are somewhat different from those of rosyface shiners from the same seine hauls among which we found adult Diptera, Hemiptera, and one ant.

Occurrence in Canada — In Ohio, *N. photogenis* is apparently decreasing in numbers in streams flowing into Lake Erie, and is not taken in the lake itself (Trautman 1957; van Meter and Trautman 1970). However, it is known in Michigan from the Huron River near Ann Arbor, and the Raisin River, Monroe County; both of these streams are tributary to Lake Erie. Primarily, silver shiners are characteristic of the Ohio River Valley, and apparently are not abundant outside that drainage system. Futhermore, the preferred habitat of silver shiners is in the deep swift riffles and current of clear streams. In view of these facts, we do not accept that silver shiners have only recently entered and crossed the lacustrine habitat of Lake Erie, especially since it is not known to have occurred in the lake (van Meter and Trautman 1970).

Although we are aware that some aquatic organisms, for example, crayfishes (Crocker and Barr 1968), have recently been introduced into Canada (probably by accident), we seriously doubt that *N. photogenis* was introduced into Ontario waters either by accident or design. At least two factors mitigate against such a possibility; firstly, the silver shiner is not a hardy species, and secondly, it is nowhere abundant north of the Ohio River Valley. For an introduction to be successful, the silver shiners would have had to survive an extended

TABLE 1. Selected morphometric and meristic data on *Notropis photogenis*, *N. rubellus*, and *N. atherinoides*. Measurements of standard length (SL), the ratios of snout length (Sn L) to orbit diameter (OD), eye–dorsal length (E–D L) to dorsal–caudal length (P–D L) and dorsal–caudal length to pelvic–caudal length (P–P L) are given for juveniles (Juv) and adults (Ad). If one count predominates in the meristic data, it is given and the range is included in parentheses.

Species	SL (*mm*)	Sn L / OD	E–D L / P–D L	P–D L / P–P L	Dorsal rays	Anal rays	Pelvic rays	Pectoral rays	Lateral line scales	Scale rows above lateral line	Vertebral centra	Pharyngeal teeth
N. photogenis Juv	32.5–54.5	≤1	≤1	≥0.91	9	11 (10–12)	9 (8)	15–17	38–41	5	40–43	1,4–4,2 2,4–4,2
Ad	57.0–108.5	>1	≤1	≥0.91								
N. rubellus Juv	19.0–33.0	<1	>1	≤0.91	9	11–12	7–8	12–14	39–41	5–6	41–43	0,4–4,2 1,4–4,1 2,4–4,2
Ad	35.5–61.0	>1	>1	≤0.91								
N. atherinoides Juv	28.0–54.0	<1	>1	≤0.91	7–8	11 (10–13)	8–9	15–17	36–40	6	38–41	2,4–4,2
Ad	55.0–70.0	<1	>1	≤0.91								

journey in a bait container (for example), an improbable, but not impossible feat.

We are of the opinion that the Grand River drainage is within the indigenous range of the silver shiner but that it had simply not been detected by previous surveys. R. M. Bailey (personal communication to CGG 1971) wrote that the silver shiner was not taken in Michigan between 1942 and 1952. It is his opinion that a low residual population had existed until favorable circumstances during 1 or a few years previous to 1952 permitted a substantial increase in the population, and that by chance, this increase coincided with collecting efforts by ichthyologists. We accept this hypothesis, and feel that somewhat parallel circumstances have occurred in the Grand River drainage.

Recently, we recorded the occurrence of two other species of fishes previously not known from Canadian fresh waters (Gruchy et al. 1973) and we accepted that one of these, *Fundulus notatus*, could have been a recent arrival by natural means. However, in the case of the second species, *Campostoma anomalum*, we felt that it must have existed in Canadian waters for some time and not been previously detected. Both *C. anomalum* and *N. photogenis* prefer swift clear streams, and it is hardly credible that two such species have recently become established in Canada. Parenthetically, the need for more detailed surveys of Canadian fresh waters is pointed out, for despite Ontario waters being studied more extensively than those of most other provinces, they have yielded three species new to the Canadian fish fauna within 2 years.

Key to Species of *Notropis* Which are Found in Canada and Have Round Scales and Nine or More Anal Rays

A	Depth of body equal to or more than length of head; with a black spot at anterior base of the dorsal fin .... *N. umbratilis*
AA	Depth of body less than length of head; without a black spot at anterior base of dorsal.......... B
B	Origin of dorsal fin over insertion of ventrals; a crescent-shaped patch of pigment medial to each nostril; mid-dorsal stripe narrow, dense, and clearly defined.......... *N. photogenis*
BB	Origin of dorsal fin posterior to insertion of ventrals; no crescent-shaped patches of pigment medial to nostrils; mid-dorsal stripe wider, not clearly defined.......... C
C	Pectoral rays 15 or 16 (exceptionally 17); lateral pigmentation terminating above lateral line; snout length less than orbit diameter throughout range of size.......... *N. atherinoides*
CC	Pectoral rays 11 to 14; lateral pigmentation terminating at or below lateral line; in specimens more than 35 mm SL snout length is greater than orbit diameter.......... *N. rubellus*

Acknowledgments — We wish to thank Drs W. B. Scott and E. J. Crossman (Royal Ontario Museum) for their cooperation in collecting and loaning specimens. They and Drs R. M. Bailey (University of Michigan) and D. E. McAllister (National Museum of Natural Sciences) have patiently argued with us about the problem of "southern" species which occur in Canada. Mr B. T. Kidd, Malacology Unit, National Museum of Natural Sciences, kindly helped during the field work.

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Computer Program for Sample Sizes Required to Determine Disease Incidence in Fish Populations

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OSSIANDER, F. J., AND G. WEDEMEYER. 1973. Computer program for sample sizes required to determine disease incidence in fish populations. J. Fish. Res. Board Can. 30: 1383–1384.

A computer program is described for generating the sample size tables required in fish hatchery disease inspection and certification. The program was designed to aid in detection of infectious pancreatic necrosis (IPN) in salmonids, but it is applicable to any fish disease inspection when the sampling plan follows the hypergeometric distribution.

OSSIANDER, F. J., AND G. WEDEMEYER. 1973. Computer program for sample sizes required to determine disease incidence in fish populations. J. Fish. Res. Board Can. 30: 1383–1384.

Nous décrivons un programme d'ordinateur produisant des tables de grandeur d'échantillons requis pour l'inspection sanitaire et la certification d'établissements de pisciculture. Ce programme est orienté surtout vers le dépistage de la pancréatite infectieuse nécrosante (PIN), mais peut servir à toute autre inspection sanitaire des poissons, pourvu que l'échantillonnage suive un plan de distribution hypergéométrique.

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MANY state and federal regulations now require that fish or fish products be inspected and certified to be free of certain infectious diseases before they can be transported across state or federal boundaries. In such inspections, it is essential to know how large a sample size to take in order to detect a given incidence of symptomatic or clinically normal, asymptomatic, carrier fish in a population.

Samples drawn without replacement from a population in which the members fall into one of two classes (e.g. diseased or healthy) is stereotypic of the basic sampling problems represented by the hypergeometric probability distribution. The most economical sampling plan is obtained by finding the minimum sample size necessary to detect at least one disease carrier in a fish population of a given total size at the desired disease incidence and Type I statistical error level.

Tabular values which would satisfy the multitude of cases that can arise in a hatchery situation are not available and the hand calculated binomial, Poisson, or normal distribution approximations to the hypergeometric are tedious and not a viable alternative for nonspecialists. Also, remote access to computers is available to many scientists and computer implementation of standard functions has become a convenient alternative to hand calculation.

This report presents a description of a computer program for generating tables of sample sizes required to detect one or more disease carriers in virtually any fish inspection situation. One such table, designed for virus (IPN) inspections of salmonids, has been in use for several years (Amend and Wedemeyer 1970).

Methods — From the hypergeometric distribution, the probability (Parzen 1960) of obtaining exactly x carriers in a sample of n fish from a total population of N fish where M of the fish are carriers is:

$$P(x) = P(x1\ \mathrm{N}, n, \mathrm{M}) = \frac{\binom{\mathrm{M}}{x}\binom{\mathrm{N}-\mathrm{M}}{n-x}}{\binom{\mathrm{N}}{n}}$$

For a disease survey, the user generally needs a solution of this equation for n, the sample size, given the other parameters of the distribution i.e. percent disease incidence to be detected and population size.

The formula provides the exact probabilities of 0, 1, 2,… of the M carriers in the population being drawn in a sample of size n. If the chance is $P(x = 0)$ of zero carriers in the sample when there are M carriers in the population, then there will be $100(1-P(x = 0))$ percent confidence that the true M is at least no more than the hypothesized M.

The probability of exactly zero events in the sample when there are M events in the population is:

$$P(x = 0) = P(01, \mathrm{N}, n, \mathrm{M}) = \frac{(\mathrm{N}-\mathrm{M})!}{\mathrm{N}!}\quad\frac{(\mathrm{N}-n)!}{(\mathrm{N}-\mathrm{M}-n)!}$$

$$= \left(\frac{\mathrm{N}-n}{\mathrm{N}}\right)\left(\frac{\mathrm{N}-n-1}{\mathrm{N}-1}\right)\cdots\left(\frac{\mathrm{N}-n-\mathrm{M}+1}{\mathrm{N}-\mathrm{M}+1}\right)$$

The following restrictions apply to the above formulas

$$0 \leq x \leq n$$
$$0 \leq x \leq \mathrm{M}$$
$$0 \leq n-x \leq \mathrm{N}-\mathrm{M}$$

For the application considered here

$$P(x \geq 1) = 1-P(x = 0).$$

Let the acceptable Type I statistical error level be A. Then

$$P(x \geq 1) = 1-\mathrm{A} = 1-P(x = 0)$$

and

$$P(x = 0) = \mathrm{A}.$$

The sample size n needs to be determined for which $P(x = 0) = \mathrm{A}$. This is accomplished by a computer program which increments the numerator and denominator of the formula for $P(x = 0)$ one unit at a time until the required value is obtained. Since n must be an integer value the actual sample size n^1 is taken for the next value of n for which $P(x = 0) < \mathrm{A}$.

The program is written in FORTRAN IV for an IBM 1130 computer with an 8 K memory. The necessary program input parameters are the population size, the disease incidence to be detected, and the Type I statistical error level. Output tables are generated and printed, listing the number of carriers for a given population size and disease incidence; these figures are subsequently used in the program to compute tables of sample size.

TABLE 1. Sample sizes (n) needed to detect at least one carrier fish in populations (N) at the given disease incidence (M), 95% confidence level.

Population size (N)[a]	Percentage disease incidence to be detected (M)						
	0.5	1.0	2.0	3.0	4.0	5.0	10.0
50	46	46	46	37	37	29	20
100	93	93	76	61	50	43	23
250	192	156	110	75	62	49	25
500	314	223	127	88	67	54	26
1,000	448	256	136	92	69	55	27
2,500	512	279	142	95	71	56	27
5,000	562	288	145	96	71	57	27
10,000	579	292	146	96	72	57	27
100,000	594	296	147	97	72	57	27
1,000,000	596	297	147	97	72	57	27
1,000,000[b] or more	600	300	150	100	75	60	30

[a] For intermediate population sizes, use sample size for next larger population listed.

[b] Sample sizes calculated from the Poisson probability distribution.

Table 1 gives an example of one of these in current use (Amend and Wedemeyer 1970) based on the 95% confidence level and 0.5% as the lowest disease incidence to be detected. The program is written so that the user can readily vary population size (N), disease incidence (M), and confidence level (A) to suit his own application. For example, a survey for *Myxosoma cerebralis* (whirling disease) would probably require more restrictive parameters than the example shown in Table I which is used for IPN. A copy of the program deck with a detailed explanatory listing and an output are available from either of the authors.

Acknowledgments — The authors appreciate the suggestions of A. Johnson and the valuable computer programming assistance provided by G. Lange.

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Growth Rates of Intertidal Molluscs as Indicators of Effects of Unexpected Incidents of Pollution

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BLACK, R. 1973. Growth rates of intertidal molluscs as indicators of effects of unexpected incidents of pollution. J. Fish. Res. Board Can. 30: 1385–1388.

Shells of living molluscs contain a record of previous growth rate if the time interval between check marks is known. The check marks in *Mytilus edulis* and *Littorina littorea* are probably annual marks. Growth rates of *Mytilus* in 1969, the year of significant elemental phosphorus pollution at Long Harbour, Newfoundland, were no different from those in preceding or succeeding years. No *Littorina* alive in 1969 occurred at Long Harbour, but they were abundant at other locations. This sort of analysis, used with caution because effects of pollutants may be confounded with effects of other variables, provides a method of examining nonlethal effects of unexpected polluting events.

BLACK, R. 1973. Growth rates of intertidal molluscs as indicators of effects of unexpected incidents of pollution. J. Fish. Res. Board Can. 30: 1385–1388.

La coquille des mollusques vivants renferme un profile du rythme de croissance passée, pourvu que soit connu l'intervalle de temps entre les marques d'arrêt de croissance. Ces marques sont probablement déposées annuellement sur la coquille de *Mytilus edulis* et de *Littorina littorea*. Le taux de croissance de *Mytilus* en 1969, année où il y eut pollution notable par le phosphore élémentaire à Long Harbour, T. -N, n'était pas différent de celui des années précédentes et suivantes. Les *Littorina* vivantes étaient absentes de Long Harbour en 1969, alors qu'elles étaient abondantes en d'autres endroits. Des analyses de cette nature, pourvu qu'elles soient utilisées avec précaution, parce que les effets des polluants peuvent facilement être confondus avec ceux d'autres variables, permettent de déterminer les effets non léthaux de pollutions accidentelles.

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THIS paper describes a method for measuring changes associated with unexpected incidents of pollution in the growth rate of molluscs. It examines the specific question: did the unusual chemical effluent containing large amounts of elemental phosphorus from the plant at Long Harbour, Nfld., have an effect on the growth in 1969 of *Mytilus edulis*, a mussel, or *Littorina littorea*, a periwinkle? These are both common, abundant intertidal molluscs that accumulate phosphorus rapidly (Fletcher 1971). Jangaard (1972) has compiled evidence about the elemental phosphorus pollution crisis at Long Harbour.

If seasonal differences in biological activity are preserved as permanent marks laid down in hard parts of an organism, then each individual contains a record of its growth history and its age. Familiar examples are tree rings and the marks in scales and otoliths of fish (Weatherly 1972 and Crisp 1971). Once the time interval between the marks is known, growth rates in previous years are easy to calculate.

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Although both Seed (1969) and Lubinsky (1958) used check marks on the shells of *M. edulis* from the eastern Atlantic and Arctic as annual marks in determinations of the ages of mussels, Harger (1967) claims that mussels produce check marks when they are physically disturbed (see also references cited by Seed 1969). I am unaware of any published information about check marks on *L. littorea*. Since Newfoundland has great extremes of air and water temperature with extremely cold winter weather from January to March, it is probable that the distinct check marks on shells of intertidal molluscs are indications of cessation of growth during these winter periods and indeed are annual marks.

The experimental treatment in the analyses presented here was the unusual chemical effluents from the phosphorus plant at Long Harbour in 1969. The years before, and to a lesser extent, the years after 1969 at Long Harbour served as one kind of a control treatment. The other control treatment was 1969 in other locations: in Placentia Bay close to Long Harbour, at Fox Harbour, and on the east coast of Newfoundland near St.

John's at Witless Bay, Quidi Vidi Gut, and Cuckold Cove.

Methods — I placed individually marked and measured *M. edulis* from Long Harbour in fiberglass window screen cages tied to intertidal sections of pier pilings to provide an exact measure of growth rate from August 25 to November 20, 1972. I examined distances from the most recent check mark to the margin of the shells of *L. littorea* collected at different times of the year in Nova Scotia to determine whether the distance increased progressively from spring to winter.

At the low water level of spring tides I collected samples of both living mussels and periwinkles from several sites at most of the locations already mentioned. At some sites mussels and periwinkles did not occur together. Using vernier calipers I measured the total length of each mussel and the length at each distinct check mark. Because the spire erodes from old periwinkles, length is a less reliable measure than shell width. For each periwinkle I measured the width of the shell at each distinct check mark and the distance between adjacent check marks at the midpoint of the shell's width. If the check marks are annual, growth during part of 1972 is represented by the distance between the margin of the shell and the closest check mark to the margin; growth during 1971 is represented by the distance between closest and second closest check marks to the margin and so on for the previous intervals. Comparisons between increment in shell size between adjacent check marks (Y) and shell size at the older check mark (X) showed that larger animals grew more slowly. This relation explained about 41% of the variance in growth rate for *Littorina* but only about 13% for *Mytilus*. For this reason I used analysis of covariance to calculate an average growth rate (adjusted Y) for each species, for each year, for particular sizes of animals: 10 mm wide for *Littorina* and 15 mm or 30 mm long for *Mytilus*. This removed the bias in the growth rate caused by differences in average size of animals between years and between locations. I obtained air temperature data for Placentia Bay and St. John's from *Monthly Record Meteorological Observations in Canada*.

Results — In 3 months 45 mussels averaging 22 mm long grew an average of 1.1 mm at Long Harbour, and 9 mussels averaging 23 mm long grew an average of 1.4 mm at Fox Harbour. Although these mussels ranged in size from 41 to 15 mm, their growth rate did not vary significantly with their size. If this 3- month period was one half of the growing season, a rough estimate of yearly growth rate of these mussels would be 2.2–2.8 mm/year. This is probably an underestimate because of the effects of caging the mussels.

The distance from the most recent check mark to the shell margin increased progressively between May and December for *L. littorea* from Nova Scotia (Table 1). This observation is consistent with the hypothesis that the check mark was produced in the winter and new growth during the next season was uninterrupted by other check marks. From these data an estimate of the yearly increase in length along the whorl of the shell of a 10-mm wide snail would be in excess of 8 mm. These estimates of yearly growth rate for *Littorina* and for *Mytilus*, for 1972, are similar to those obtained by using the distances between check marks to calculate rates for previous years (Table 2).

TABLE 1. Distance from most recent check mark to shell margin for *Littorina littorea*. The average distance is adjusted by analysis of covariance for a periwinkle 10 mm wide, from comparisons between the distance from check mark to shell margin (Y) and width of shell at the check mark (X). Values at successive dates are significantly different from each other ($P<0.05$). Sample sizes are in parentheses.

Date	Location of *L. littorea* in Nova Scotia		
1972	Chain Rock, Halifax	Bedford Basin	Peggy's Cove
May 1		1.1 mm (11)	
May 23	3.0 mm (57)		7.4 mm (18)
July 8	4.8 mm (55)	7.0 mm (40)	10.7 mm (54)
27 Sept.	9.6 mm (39)		
13 Dec.		8.3 mm (44)	

Growth rates calculated from check marks for *M. edulis* at Long Harbour in 1969 were not unusual in comparison with other years. Mussels grew at the slowest rate in a different year at each site (Table 2). This was also the pattern at Witless Bay. These data demonstrated no association of growth rate per year among sites at Long Harbour or at Witless Bay (Kendall's coefficient of concordance). *Mytilus* did, however, grow at a faster rate at Long Harbour than at the other locations.

Littorina littorea were abundant at Long Harbour but no animals were large and none were old enough to have been set before 1969 or 1970, so no comparisons between growth rates in 1969 and other years were possible. At other locations, the pattern of growth rates from year to year was dissimilar among sites at the same location (Spearman's rank correlation for Fox Harbour and Kendall's coefficient of concordance for Witless Bay).

Part of the differences between years in growth rate of mussels and periwinkles was associated with summer air temperatures between May and October for animals near St. John's. Mussels grew more slowly in years of high summer air temperatures ($r = -.96$, $n=5$, $P<0.01$), while periwinkles grew more slowly in years of low summer temperatures ($r = +.90$, $n=5$, $P<0.05$). In Placentia Bay, growth rates were not associated with summer air temperatures.

Discussion — Because polluting events are often unexpected, data describing conditions before the event rarely exist to serve as a control in assessment of the effects of the event. Organisms surviving and remaining at the site of the polluting event can provide information about nonlethal effects. For example, *Nucella lapillus* stopped growing, thickened its shell margin and produced a row of teeth when an oil detergent reduced the snail's food supply (Byran 1969).

The present study points out some difficulties of using check marks as records of growth histories to detect effects of pollution. First, the time interval between the check marks is essential information which can be obtained by close observation of growing animals. My observations on *Littorina* are more convincing than those on *Mytilus*, but together with the claims by Seed (1969) for *Mytilus*, they

TABLE 2. Growth rates in millimeters per year calculated by analysis of covariance from comparisons of yearly increase in shell dimension (Y) with initial shell dimension (X). For *Littorina* X is shell width, and Y is the distance between check marks along the whorl of the shell. For *Mytilus* X is the shell length and Y is the distance between successive check marks.

		Growth rate of shells (mm/year) (sample size in parentheses)									
		L. littorea 10 mm wide					*M. edulis* 15 mm long[d]				
Location	Sampling site	1967	1968	1969	1970	1971	1967	1968	1969	1970	1971
Long Harbour[a]	1				9.3 (8)	8.9 (25)	7.2 (19)	6.3 (21)	5.3 (24)	4.1* (28)	6.1 (45)
	2			2.2 (3)	6.9 (7)	6.4 (18)		2.7 (9)	4.2 (16)	4.6 (36)	5.7 (52)
	3					2.2 (3)	7.1* (13)	4.4 (20)	4.9 (25)	4.6 (27)	3.3 (27)
Fox Harbour	1		7.3 (17)	8.5 (18)	7.9 (29)	7.0 (36)					
	2		6.5 (6)	6.9 (11)	7.8 (17)	7.6 (33)					
	3									2.2 (11)	4.9 (24)
Witless Bay	1	8.7 (11)	8.1 (15)	9.3* (24)	18.2 (13)	15.7 (29)	2.9 (11)	2.6 (23)	2.3 (46)	2.3* (56)	1.6 (60)
	2[b]		6.2 (6)	13.9 (8)	11.3 (35)	12.0 (63)	3.3 (12)	3.4 (35)	3.1* (62)	2.8 (84)	2.5 (97)
	3		14.0 (6)	13.5 (14)	10.4 (18)	10.6 (23)	3.0 (3)	3.5 (9)	3.0 (16)	3.3 (25)	2.6 (29)
Quidi Vidi Gut[c]									2.5 (10)	2.8 (16)	2.9 (39)
Cuckold Cove				6.4 (9)	6.3 (19)	6.3 (27)				2.0 (4)	0.8 (20)

[a] Long Harbour is location of elemental phosphorus spill in 1969.
[b] Witless Bay site is close to a fishmeal plant and the wastes from it discolor the shore here.
[c] Quidi Vidi Gut has a domestic sewage outfall entering it.
[d] Long Harbour *Mytilus* 30 mm long.
* Years have significantly different growth rates by analysis of covariance. Asterisk is adjacent to a year with significantly lower growth rate, or is between years with significantly different rates, $P<0.05$.

suggest that the check marks on both species are annual ones.

Second, effects of polluting events will always be confounded with effects of other factors. The heterogeneity of growth rates among sites at the same location in the same year is one indication of this, and the association between years with physical parameters such as temperature is another. Replicated sampling of animals in similar conditions of exposure, density, and tidal level is necessary.

In the data presented here, the effects of the Long Harbour phosphorus plant effluents are apparently not recorded as a decrease in growth rate of *M. edulis*. The absence of *L. littorea* old enough to have been alive before the spill suggests that the periwinkles were killed in the same year as the spill, but whether the phosphorus was the cause is indeterminable. Periwinkles do absorb at least three times as much phosphorus as mussels after a 48-h exposure to 15 μg/liter of elemental phosphorus (Fletcher 1971). Perhaps periwinkles can receive lethal doses of phosphorus faster and at lower environmental concentrations than mussels can.

Although the use of growth check marks on mollusc shells is not an entirely satisfactory way of examining effects of past polluting events, in some instances it may be the only available method. *Littorina littorea* is a good choice for this purpose because its check marks are more distinct than those of *M. edulis* and the closer relation between growth rate and size of the animal make comparisons more reliable for *Littorina* than for *Mytilus*.

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Reliability of an Ammonia Probe for Electrometric Determination of Total Ammonia Nitrogen in Fish Tanks

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BARICA, J. 1973. Reliability of an ammonia probe for electrometric determination of total ammonia nitrogen in fish tanks. J. Fish. Res. Board Can. 30: 1389–1392.

The method involves an alkalization of a sample to *p*H 12 and subsequent measurement of liberated un-ionized ammonia with a gas-permeable membrane electrode. Total ammonia is measured directly rather than ammonium ion. Tests on different samples of water from aquaria and fish tanks showed a mean absolute difference of ±8.3% as compared with the phenolhypochlorite method in the concentration range of 0.5–5.1 mg/liter NH_3-N. The lowest level of detection was 0.1 mg/liter NH_3-N.

BARICA, J. 1973. Reliability of an ammonia probe for electrometric determination of total ammonia nitrogen in fish tanks. J. Fish. Res. Board Can. 30: 1389–1392.

Nous décrivons une nouvelle méthode électrométrique de dosage de l'azote ammoniacal total dans des échantillons d'eau de viviers à poissons. Cette méthode comporte une alcalinisation de l'échantillon à un *p*H de 12, suivie du dosage de l'ammoniac non ionisé à l'aide d'une électrode à membrane perméable au gaz. L'ammoniac total, plutôt que l'ion ammonium, est mesuré directement. Des mesures effectuées sur différents échantillons d'eau provenant d'aquariums et de viviers démontrent une différence absolue moyenne de ± 8.3%, comparativement aux valeurs obtenues par la méthode du phénol-hypochlorite, sur une gamme de concentrations de 0.5 à 5.1 mg/litre de NH_3–N. Le seuil inférieur de détection est de 0.1 mg/litre de NH_3–N.

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IN a recent note (Barica 1971) a simplified method for determining ammonium ion in water with a univalent cation glass electrode was described. Although this method was fast and suitable for untreated water samples with ammonium–nitrogen content higher than 0.5 mg/liter (fish tanks, hypolimnetic lake water), its application was limited to samples with constant sodium and potassium background because the glass electrode was sensitive to these cations also. New gas-membrane electrodes have recently appeared on the market which are sensitive to un-ionized ammonia in solution and are apparently more specific and subject to less interferences than the glass electrode. In addition, they do not require a separate reference electrode, as the electrode system represents itself an electrochemical cell (hence the term "probe").

This report evaluates the usefulness and reliability of the Orion ammonia electrode model 95–10 (Orion Research Inc., Cambridge, Mass.) for a direct determination of total ammonia in fish-holding tanks and aquaria and its applicability for routine analytical work.

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Theory of operation — The ammonia probe is a gas-sensing electrode, which detects un-ionized ammonia gas in aqueous solution. It is a combination type of electrode, with reference sensor incorporated internally and therefore not requiring a separate reference electrode. It functions as if it were a specific ion electrode following the Nernstian law.

Ammonia diffuses through a hydrophobic gas-permeable membrane until the partial pressure of ammonia is the same on both sides of the membrane and reacts with water in the electrode filling solution to produce ammonium and hydroxyl ions

$$NH_3 + H_2O \rightleftharpoons NH_4^+ + OH^-$$

The released hydroxyl ions change the *p*H of the internal filling solution. Since the relation between ammonia, ammonium, and hydroxide is formulated as:

$$\frac{[NH_4^+]\,[OH^-]}{[NH_3]} = \text{constant}$$

and the internal filling solution contains NH_4Cl at a sufficiently high level so that the NH_4^+ is considered fixed, the *p*H change of the internal solution gives indirectly the ammonia concentration

$$[OH^-] = NH_3 \cdot \text{constant}$$

which is detected by electrode internal reference sensing element in a Nernstian manner (Orion 1971).

Electrode characteristics — pH adjustment — Since the probe detects only ammonia gas and is entirely insensitive to ammonium ions, a complete conversion of ammonium ions to the un-ionized ammonia form by *p*H adjustment is necessary to obtain a measure of total ammonia nitrogen. From the ionization constant it follows that at *p*H 11 and higher practically all ammonium will be present in an un-ionized ammonia form. Therefore, when the *p*H of the sample is adjusted between 12–13 the reading will correspond to total ammonia nitrogen, i.e. the sum of ammonium and ammonia nitrogen. To minimize dilution error, a strong solution of NaOH (10 M or 40%) added in the amount of approximately 1 ml/100 ml of the sample is recommended. The optimum amount of NaOH for different types of natural waters might vary and be slightly higher for hard waters, and should be determined experimentally for the particular type of water. In our work 1 ml of 40% NaOH proved to be sufficient to bring *p*H to about 12 in three different types of water with specific conductance values from 890 to 1880 µmhos/cm at 25 C.

Electrode response to ammonia in natural water — The electrode response to ammonia in alkaline solution of NH_4Cl follows the Nernstian slope only between concentrations 10^{-1} to 10^{-4} M (14 g/liter to 14 mg/liter NH_3-N, Fig. 1.) In the normal working range of fish-holding tanks and aquaria (0.3 to 2 mg/liter NH_3-N) the response does not follow the Nernstian equation. Preparing working calibration curves in this range is therefore essential. Figure 2 shows some typical electrode responses in the concentration range of 0.1 to 10 mg/liter NH_3-N. As can be seen, the data for concentrations of 0.5 mg/liter NH_3-N and higher are linear when presented on a semi-log plot, but are slightly displaced vertically for different types of natural waters and different ionic strengths. It is therefore advisable to use fresh aquarium make-up water (normally ammonia-free) rather than distilled water for preparation of calibration curves. Two to three known ammonia concentrations are sufficient to draw a reliable calibration curve for ammonia readout (Fig. 2, curve 4). As any specific ion electrode, the ammonia probe develops a potential drift as a result of temperature changes and aging of membrane and filling solution. The calibration should be performed at the same temperature (± 2 C) as the water samples, at least once a day. When used in hatcheries or laboratories, make-up water and the fish tanks are usually at the same temperature.

Speed of response — Since the probe requires a diffusion of NH_3 gas through the membrane from the alkalized sample, the response in somewhat slower than

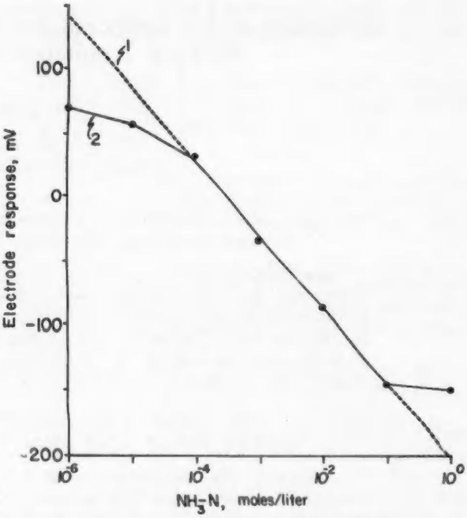

FIG. 1. Electrode responses to different molarities of ammonia. 1 — theoretical Nernstian response; 2 — actual response in pure solution of NH_4Cl.

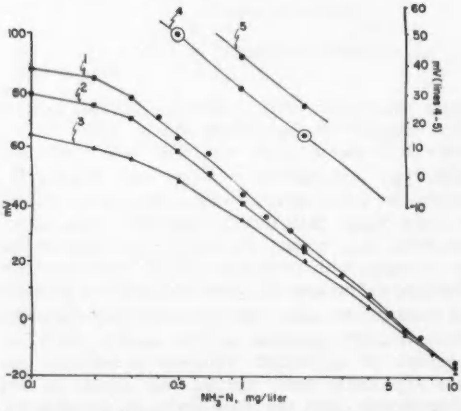

FIG. 2. Electrode response for different types of water in the concentration range of 0.1–10 mg/liter NH_3-N. 1 — distilled water; 2 — Winnipeg tap water (spec. cond. 920 µmhos/cm at 25 C); 3 — the Assiniboine River water (spec. cond. 1880 µmhos/cm at 25 C); 4 — Rockwood Hatchery make-up water (spec. cond. 890 µmhos/cm at 25 C); 5 as 4, with a replaced membrane in the electrode; note the electrode drift. Concentrations adjusted by known additions of standard NH_4Cl. Lines 4 and 5 are recommended calibration curves for working range of total ammonia level expected in fish tanks.

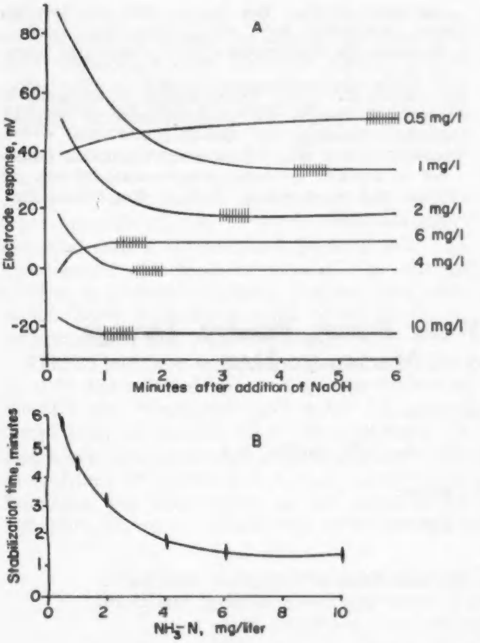

FIG. 3. Electrode response as a function of time for various concentrations of total ammonia. A, electrode responses; stabilization time shown by shaded areas; B, stabilization time versus total ammonia concentration. Readings were taken in 15-sec intervals.

it was in the case of the glass electrode, but it increases with concentration of ammonia in the sample. Figure 3 shows response curves to various levels of ammonia between 0.5 to 10 mg/liter. The low levels (around 1 mg/liter) require about 5 min before the reading stabilizes.

Verification of method—Several series of water samples from different aquaria, hatchery and fish-holding tanks in the Freshwater Institute were analyzed for total ammonia nitrogen, using simultaneously the ammonia probe and the conventional spectrophotometric phenolhypochlorite method (Solórzano 1969) in an automated version. The results of both determinations are compared in Table 1. It follows that the ammonia probe was unsuitable for concentrations below 0.1 mg/liter NH_3-N, and in the range of 0.2 to 0.5 mg/liter NH_3-N yielded results differing from those found by the phenolhypochlorite method by ± 17%. In the concentration range 0.5 to 5.1 mg/liter NH_3-N the absolute mean difference was ± 8.3%.

TABLE 1. Mean difference between concentrations of total ammonia nitrogen in fish tanks found by ammonia probe and those determined by phenolhypochlorite method.

Concn range (*mg/liter* *NH_3-N*)	No. samples	Mean absolute difference (± %)	Range percent difference
0–0.1	10	69.5	+3.8 to +166
0.1–0.2	11	16.9	−30.5 to +23.6
0.2–0.5	8	17.1	−56.7 to +44.4
0.5–1.0	9	8.8	−30.5 to + 1.9
1.0–5.1	16	7.8	−16.6 to + 9.0

Proposed methodology — Apparatus — Ammonia probe (Orion model 95–10 or comparable electrode); Millivolt meter (Orion model 801 Digital *p*H Meter or comparable *p*H meter with a millivolt scale); Magnetic stirrer.

Reagents — Standard ammonia solution. Dissolve 3.818 g anhydrous ammonium chloride, dried at 105 C in deionized water and dilute to 1000 ml. 1 ml = 1 mg NH_3-N.
Sodium hydroxide, 40%. Add deionized water to 400 g of NaOH and make to approximately 1000 ml. Cool in a coldwater bath during mixing.

Procedure — Use approximately 100 ml of sample (120–150-ml beaker) and introduce the ammonia probe. Stir the solution at a constant rate. Add approximately 1 ml of 40% NaOH. After 5 min, record the electrode potential. To prevent solution carryover, the probe should be rinsed in deionized water and dried with a tissue between measurement of different samples.
To prepare the calibration curve, use exactly 100 ml of deionized water, add approximately 1 ml of 40% NaOH and introduce the ammonia probe into the solution. With a micropipette or dispensing microsyringe add 0.05 ml ammonium chloride standard solution to obtain an ammonia level of 0.5 mg/liter NH_3-N. Stir the solution at a constant rate and after 5 min record the potential. Add 0.15 ml more of ammonium chloride standard solution (total ammonia level of 2.0 mg/liter NH_3-N) and obtain a measurement in the same way. Plot the potentials for 0.5 and 2.0 mg/liter NH_3-N, respectively, on a semi-log graph paper and draw a straight line. This calibration curve is good for concentrations of 0.3–5 mg/liter NH_3-N. If a different range is expected, adjust the calibration concentrations accordingly. The concentrations of total NH_3-N can be read from this to the nearest tenth of a milligram. If relative amounts of ammonium ion and free un-ionized ammonia are required,

measure the *p*H of sample separately and use appropriate methods of calculation (Trussell 1972).

Acknowledgments — I am indebted to E. Pessah and D. Spriggs for supplying the fish-tank samples and to R. K. Schade for analytical assistance. S. T. Zettler and C. Boyce prepared the drawings.

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Supersaturation of Nitrogen in Water During Passage Through Hydroelectric Turbines at Mactaquac Dam

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MACDONALD, J. R., AND R. A. HYATT. 1973. Supersaturation of nitrogen in water during passage through hydroelectric turbines at Mactaquac Dam. J. Fish. Res. Board Can. 30: 1392–1394.

Two fish kills occurred at the Saint John River, New Brunswick, below the Mactaquac Hydroelectric Station in the summer of 1968. Gas bubbles, commonly associated with nitrogen supersaturation, were observed on dead and dying salmon (*Salmo salar*) and eels (*Anguilla rostrata*). Tests showed that the concentrations of dissolved oxygen and nitrogen gases were substantially increased when water passed through the turbine generating system at low generating levels. Concentrations of dissolved nitrogen gas increased by as much as 20% above atmospheric equilibrium.

MACDONALD, J. R., AND R. A. HYATT. 1973. Supersaturation of nitrogen in water during passage through hydroelectric turbines at Mactaquac Dam. J. Fish. Res. Board Can. 30: 1392–1394.

Des mortalités se sont produites en deux occasions dans la rivière Saint-Jean, Nouveau-Brunswick, en aval de la centrale électrique de Mactaquac à l'été 1968. Des bulles de gaz, communément associées à une sursaturation d'azote, ont été observées chez des anguilles et des saumons morts ou mourants. Des essais ont démontré que les teneurs en oxygène dissous et en gaz d'azote augmentent considérablement quand l'eau passe dans les turbines génératrices, à de bas niveaux de production. La teneur en azote dissous augmente jusqu'à dépasser de 20% l'équilibre atmosphérique.

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Two fish kills were observed at the Saint John River, New Brunswick, below the Mactaquac Hydroelectric Station in the late summer of 1968. The adult Atlantic salmon (*Salmo salar*) and eels (*Anguilla rostrata*) were the species most severely affected. It was estimated that 200 salmon, or 10% of the 1968 upriver run, were killed as they approached Mactaquac fish collection facilities. The dead and dying fish were observed mainly in the more shallow part of the river immediately below the tailrace basin, although dying salmon were observed 1 mile below the tailrace. Dead and dying salmon exhibited bubbles of clear gas under the skin which covers the fins, or under the connective tissue which surrounds the viscera, or both. The eels had accumulations of gas under the skin of the

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head region. The dead fish exhibited no other visible signs of disease or injury. No dead fish were observed upriver from the dam. The fish kills occurred during weekend periods when only one generating unit was operating at or near the 5-Mw minimum capacity. The first dead salmon were observed approximately 24 hr after the reduction in generating level.

Gas-bubble formation in fish commonly results from exposure of fish to water which is supersaturated with air (Marsh and Gorham 1905). An investigation was therefore initiated in an attempt to identify a source of supersaturation of air gases in the Saint John River water either above, at, or immediately below the Mactaquac Dam.

Rainfall had been extremely light in the summer of 1968 and hence no water had been discharged through the Mactaquac spill gates for several weeks prior to the fish kills. This eliminated the possibility of supersaturation during spillage, such as described by Harvey and Cooper (1962) or by Beiningen and Ebel (1970), as the cause of the fish kills. However, during the investigations it was observed that large quantities of air bubbles periodically welled up in the "turbine boils" in the Mactaquac tailrace basin. The following study was then made to determine if the generating water which passed through the turbines was being supersaturated with air during passage.

Methods — Samples of water were collected from the headpond and from the turbine boils in the tailrace during different generating load levels. The first set of samples was analyzed by the modified Winkler Method in an effort to determine, by comparing dissolved oxygen concentrations, if the river water was undergoing superaeration during passage from the headpond through the turbines. The second series of samples was analyzed for dissolved oxygen by the modified Winkler Method and for dissolved nitrogen concentrations using a microgasometric analyzer as described by Scholander et al. (1955). Each test result was based on a single measurement.

The Scholander analyzer was checked for accuracy by measuring the concentrations of nitrogen gas in distilled water which had been aerated for 48 hr. Seven determinations yielded an average of 101% of saturation of nitrogen with all results falling within a range of

TABLE 1. Concentrations of dissolved oxygen (D.O.) in Mactaquac headpond and tailrace at four different levels of hydroelectric power generation. Only one generating unit in operation during tests.

	Generating level	Depth (*m*)	D.O. (*mg/liter*)	Temp. (*C*)	Sat. (%)
Headpond water		5	8.03	7	66
Headpond water		14	8.13	7	67
Tailrace water	5 Mw[a]	1	11.16	8	93
Tailrace water	9 Mw[a]	1	11.20	8	93
Tailrace water	15 " [a]	1	9.82	8	82
Tailrace water	35 " [a]	1	8.51	8	72

[a] 5, 9, 15, and 35 Mw power generated with approximately 1900, 2300, 2800, 4400 ft^3/sec, respectively.

TABLE 2. Concentrations of dissolved oxygen (D.O.) and nitrogen (D.N.) in Mactaquac headpond and tailrace at two levels of hydroelectric power generation. One generator operating.

	Generating level (*Mw*)	Depth (*m*)	Temp. (*C*)	D.O.		D.N.	
				mg/liter	% sat.	mg/liter	% sat.
Headpond water		1	12	7.23	66	18.17	105
Tailrace water	10	1	12	8.53	78	20.57	118
Tailrace water	10	1	12	8.75	80	21.66	125
Tailrace water	33	1	12	7.75	70	18.61	107

99–103%. A similar series of seven tests on aerated Saint John River water averaged 104% of saturation with a range of 102–106%. The results of these tests indicated that the Scholander method was sufficiently accurate for our purposes. The tests also indicated that the nitrogen saturation level for Saint John River water (as measured with this apparatus) was 104% of the theoretical level (Handbook of Chemistry 1967).

Results — The first test series conducted in November, 1968 yielded the results presented in Table 1.

The data of the first test series showed that the dissolved oxygen concentration of the generating water increased from approximately 8 mg/liter (66% saturation) to over 11 mg/liter (93% saturation) during passage through the turbine system at the lower generating levels. As the generating level increased above the 9-Mw level, the degree of aeration declined.

The second series of tests was conducted in June 1969. The data from these tests are presented in Table 2.

Dissolved oxygen concentrations increased from 66% saturation to approximately 80% saturation as the water passed through the turbines at the lower generating levels, again indicating that water passing through the turbine system at low generation levels was being aerated. The dissolved nitrogen concentration of the headpond water was measured at 105% of theoretical saturation. This saturation level is consistent with the results of the preliminary tests on nitrogen saturation of Saint John River water reported above. Tailrace water was 118 and 125% saturated with dissolved nitrogen in the two tests conducted at the 10-Mw generating level. As the generating load increased to 33 Mw, both dissolved nitrogen concentrations and dissolved oxygen concentrations of tailrace water approached the concentrations found in the headpond.

Discussion — The results of the tests indicated that the water of the Saint John River in the impoundment above the Mactaquac Dam contained subsaturation levels of dissolved oxygen, probably due to the heavy load of organic pollutants, and contained dissolved nitrogen gas approximately at saturation level. The tests further show that by the time the water reached the tailrace by way of the turbine system at low generating levels, concentrations of oxygen and nitrogen had both increased. Personnel of the New Brunswick Electric Power Commission confirmed the results when they explained that at low generating levels, air was vented into the turbine system to reduce negative pressures. The two fish kills below Mactaquac Dam had occurred during weekend periods of sustained low generating levels, at or near the 10-Mw level, when the pressure venting system would have been extensively used.

Supersaturation of generating water with air gases as the cause of gas-bubble formation in fish may not be uncommon but no reference to this phenomenon was found in the literature. Lindroth (1957) did report on tests conducted at Bergeforsen in Sweden and found that no supersaturation occurred in water that had passed through turbines. The results of this study might be of value to other investigators of gas bubble-caused fish kills.

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Métabolisme de l'iode et de la thyroxine chez *Perca flavescens*[1]

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Bibor, V., et C. Leray. 1973. Métabolisme de l'iode et de la thyroxine chez *Perca flavescens*. J. Fish. Res. Board Can. 30: 1395–1398.

La fonction thyroïdienne de *Perca flavescens* a été explorée au moyen de deux molécules marquées ($\mathrm{Na}^{125}\mathrm{I}$ et $\mathrm{T}_4{}^{125}\mathrm{I}$). Il n'a été retrouvé dans la zone glandulaire qu'une fraction hormonale marquée peu importante (4% de la radioactivité thyroïdienne 5 jours après injection de $\mathrm{Na}^{125}\mathrm{I}$) mais la mise en évidence d'un maximum d'incorporation dans les premières 24 h suggère l'existence d'un pool hormonal à renversement rapide. De plus, l'incorporation intense et rapide d'iodures dans les précurseurs (60% de MIT + DIT, 12 h après injection de $\mathrm{Na}^{125}\mathrm{I}$) traduit une activité biosynthétique importante. Au niveau périphérique, le dégradation rapide de $\mathrm{T}_4{}^{125}\mathrm{I}$ ($t\frac{1}{2} = 6$ h dans le plasma) vient appuyer ces conclusions. Les iodures présentent, dans nos conditions expérimentales, une demi-vie de 4 jours à la fois dans le sang et dans la totalité du corps. Après injection de $\mathrm{Na}^{125}\mathrm{I}$, le $\mathrm{PBH}^{125}\mathrm{I}$ présente deux maxima précoces suivis d'une augmentation progressive.

Si le deuxième maximum correspond à la sécrétion des hormones synthétisées 6 à 12 h auparavant dans la thyroïde, au sein du pool à renversement rapide, le premier maximum (6 h seulement après injection de $\mathrm{Na}^{125}\mathrm{I}$) ne peut être relié à aucun phénomène connu chez les poissons.

Bibor, V., et C. Leray. 1973. Métabolisme de l'iode et de la thyroxine chez *Perca flavescens*. J. Fish. Res. Board Can. 30: 1395–1398.

Two radioisotopes ($\mathrm{Na}^{125}\mathrm{I}$ and thyroxine^{125}I) were used to investigate thyroid function in *Perca flavescens*. In the thyroid, if the hormonal fraction is very small (4% of total radioactive thyroid components, 5 days after injection of $\mathrm{Na}^{125}\mathrm{I}$) the variation of this fraction with time suggests the existence of a rapid turnover of hormones (maximum level before 24 hr). The rapid incorporation of iodine into iodotyrosine compounds by the thyroid (60% of MIT + DIT after 12 hr) also suggests the involvement of a very important biosynthetic activity. At peripheral levels the rapid metabolism of $\mathrm{T}_4{}^{125}\mathrm{I}$ ($t\frac{1}{2} = 6$ hr in the blood) confirms this view. In the plasma, the level of labelled hormones goes through two maxima followed (48 hr after injection of $\mathrm{Na}^{125}\mathrm{I}$) by a steady increase. The second maximum observed is probably due to the release of thyroid hormones into the blood, but the first (6 hr after injection of $\mathrm{Na}^{125}\mathrm{I}$) cannot be related to any known physiological process in fishes. The half-life of ^{125}I in the plasma is the same as that in the whole body (4 days).

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Le rôle physiologique de la thyroïde chez les Poissons reste toujours imprécis et les recherches sur le fonctionnement de la glande elle-même gardent tout leur intérêt. En effet, cet aspect du problème, par la nature et l'ampleur des modulations de l'activité glandulaire, est relié au déterminisme des synthèses hormonales et doit conduire à la découverte des organes ou structures cibles. La thyroïde de *Perca flavescens*, poisson abondant dans le fleuve Saint-Laurent, ne semble avoir fait l'objet d'aucune investigation quant à son fonctionnement de base. Aussi, avons-nous procédé à une exploration générale du métabolisme de l'iode (injection de $\mathrm{Na}^{125}\mathrm{I}$) et de la thyroxine (injection de $\mathrm{T}_4{}^{125}\mathrm{I}$). Ces recherches préliminaires ont permis d'estimer plusieurs critères d'activité glandulaire et l'étude cinétique de phénomènes soit biosynthétiques soit cataboliques a révélé plusieurs aspects originaux. Le taux de renouvellement rapide des composés iodés au niveau thyroïdien semble aller de pair avec un faible taux hormonal intraglandulaire et accompagne une intense dégradation périphérique

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de T_4. Ces premiers résultats infirment donc la thèse d'une thyroïde peu active qu'une étude restreinte à certains critères suggérerait.

Matériels et méthodes — Les animaux (10 à 100 g) utilisés ici proviennent du lac Saint-Louis (élargissement du Saint-Laurent dans la région de Montréal). Après une stabulation à jeun de 1 à 12 jours en eau courante déchlorée, à température voisine de celle des eaux du fleuve et sous photopériode naturelle, on procède à une injection intrapéritonéale de 5 μC de $Na^{125}I$ dans du NaCl à 6‰ ou de 1 μC de $T_4{}^{125}I$ (A.S. = 5 $\mu C/\mu g$) dans du propylène glycol à 50%. Après le délai prévu (de 1 à 120 h), le sang est prélevé sur héparine au niveau du coeur ou de l'artère caudale. Les organes (thyroïde, muscle, foie, estomac, vésicule biliaire et intestin) sont disséqués et leur radioactivité (R.A.) est mesurée. Le pourcentage de la dose injectée, retrouvée dans le sang et le muscle, est ramené à un poids corporel idéal de 100 g (Higgs et Eales 1971); les paramètres de l'activité thyroïdienne étudiés sont: le rapport T/S; le taux plasmatique de conversion hormonale ($PBH^{125}I$): pourcentage de la fraction III isolée selon Blanquet et al. (1960). Au niveau de la thyroïde, l'analyse des composés iodés (MIT + DIT et T_3+T_4) est effectuée selon un protocole voisin de celui de Backer et al. (1967).

Résultats et discussion — L'analyse de la cinétique donne des renseignements précis sur les étapes importantes des synthèses thyroïdiennes (Fig. 1). Le rapport T/S croît lentement, mais atteint une valeur assez importante au bout de quelques jours (T/S=30 après 5 jours). La cinétique de ce phénomène montre une première phase très nette traduisant un turnover rapide (T/S = 4 après 6 h) suivie d'une augmentation de près de 2 fois (T/S = 9 après 24 h) précédant l'augmentation régulière du gradient de concentration en iode entre thyroïde et plasma. L'organification des iodures en iodotyrosines atteint une forte valeur (60% de la R. A. thyroïdienne) 12 h après l'injection de $Na^{125}I$, mais la quantité de précurseurs marqués reste stable, ce qui semble traduire un équilibre précoce avec la fraction hormonale, formée à un taux apparemment plus lent. En réalité, si cette dernière fraction iodée ne compte que pour 4% de la R.A. thyroïdienne, même après un temps assez long, l'étude chronologique révèle un pool hormonal à renversement rapide correspondant à un marquage comparativement important (6.1% de la R.A. thyroïdienne 12 h après l'injection, comparés à 1.8% après 6 h, $P<0.001$). Une analyse plus précoec de ces phénomènes a été réalisée chez des animaux préalablement à jeun depuis 12 jours (Fig. 2). Malgré le décalage des événements (provoqué peut-être par l'écart thermique ou le jeûne) et les valeurs réduites (interférence du jeûne, résultats inédits), le marquage des hormones dans la thyroïde est réalisé en deux étapes successives comme précédemment.

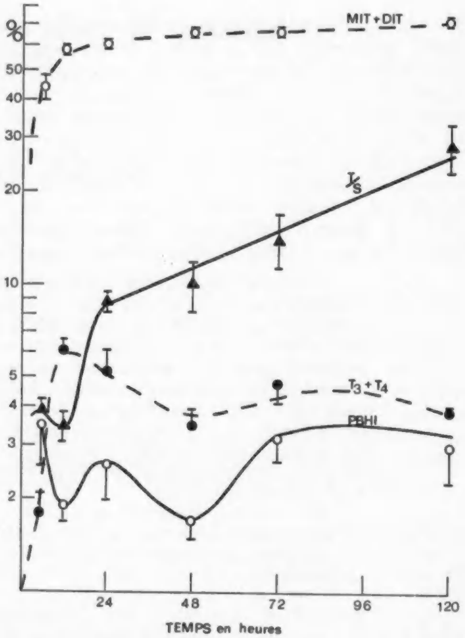

FIG. 1. Evolution chronologique des paramètres d'activité thyroïdienne. Résultats en pourcentage aux niveaux thyroïdien (MIT + DIT, T_3 + T_4) et plasmatique (PBHI). Chaque point représente la moyenne (avec son erreur standard) obtenue chez cinq animaux (poids moyen: 15 g), septembre 1972, 18 C. Injection de $Na^{125}I$ le jour de la capture.

Au niveau du plasma, le taux d'hormones marquées $PBH^{125}I$) présente deux maxima précoces d'activité, très distincts (Fig. 1 et 2), précédant une élévation progressive du taux de marquage (après 48 h, Fig. 1). Peut-être à cause d'une utilisation périphérique plus faible, c'est chez les animaux à jeun depuis plus longtemps (12 jours, Fig. 2) que le phénomène est plus net ($PBH^{125}I$ significativement différents ($P<0.001$) entre 1 h et 6 h, 6 h et 12 h, 12 h et 48 h). Si la deuxième vague d'incorporation d'iode radioactif peut être assimilée à l'apparition dans le sang des hormones synthétisées précocement au sein du pool intrathyroïdien à renversement rapide et décelable 6 ou 12 h après l'injection, la première vague, décelable dès la première heure, ne peut être assimilée à aucun phénomène déjà décrit chez les poissons.

L'analyse du mode de dégradation périphérique d'hormones marquées (T_3 ou $T_4{}^{125}I$) constitue un

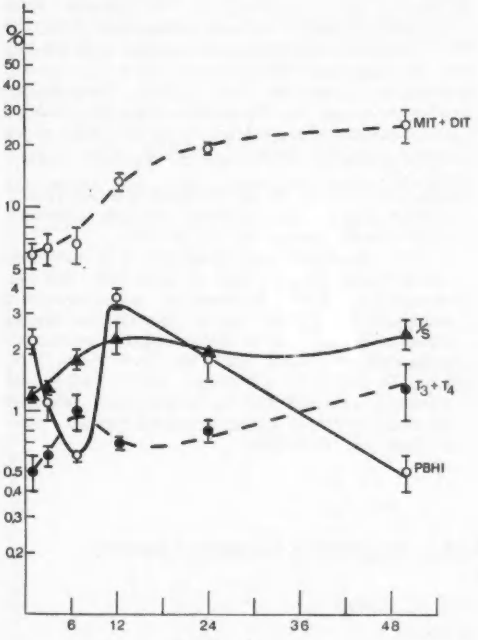

FIG. 2. Evolution chronologique rapide des paramètres d'activité thyroïdienne. Résultats en pourcentage aux niveaux thyroïdien (MIT + DIT) et plasmatique (PBHI). Chaque point représente la moyenne (avec son erreur standard) obtenue chez quatre animaux (poids moyen: 10 g), août 1972, 22 C. Injection de $Na^{125}I$ 12 jours de jeûne après la capture.

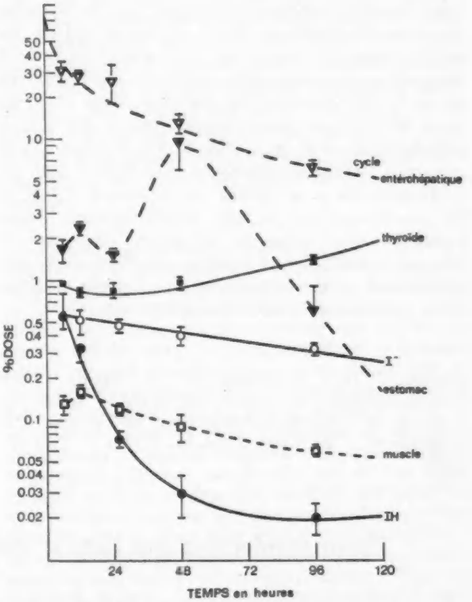

FIG. 3 Cinétique de la répartition de $T_4{}^{125}I$ dans différents organes et dans le sang. Résultats en pourcentage de la dose injectée (pour le sang et le muscle: % dose par ml ou g et correction pour poids corporel de 100 g). I^-: iodures sanguins, IH: iode hormonal (fraction III de Blanquet). Chaque point représente la moyenne (avec son erreur standard) obtenue chez cinq animaux (poids moyen: 15 g), août 1972, 21 C. Injection le jour de la capture.

moyen indirect mais très significatif d'estimer l'importance de la fraction thyroïdienne. Chez *P. flavescens* (Fig. 3), la diminution du $PBHI^{125}I$ après injection de $T_4{}^{125}I$ (demi-vie de 6 h) traduit une dégradation biologique plus rapide que chez les autres espèces déjà explorées de ce point de vue (Eales 1972). Les iodures sanguins n'ont qu'une demi-vie de 4 jours, se rapprochant ainsi des valeurs publiées pour d'autres espèces. Par comptage in vivo d'animaux entiers injectés avec 1 μC de $Na^{125}I$, nous avons pu confirmer cette valeur (résultats inédits). Après injection de $T_4{}^{125}I$, on retrouve chez *P. flavescens* une part importante de la R.A. dans les organes constituant le cycle entéro-hépatique (foie, vésicule biliaire et intestin) (Fig. 3). La vésicule biliaire contribue à elle seule pour les ¾ de la R.A. présente dans cet ensemble d'organes après 24 h. Ceci semble donc confirmer l'hypothèse d'Eales (1970) attribuant au cycle entéro-hépatique des poissons carnivores un rôle important dans l'élimination des hormones.

Au niveau musculaire, la R.A. décroît avec une demi-vie de 40 h, mais une signification physiologique ne pourra être assignée à ce phénomène qu'après vérification de la nature des substances mises en jeu.

Les différences au niveau des méthodes et des conditions expérimentales rendent difficile la comparaison de ces données obtenues chez *P. flavescens* avec celles publiées antérieurement chez d'autres Téléostéens d'eau douce (Gorbman 1959; Drury et Eales 1968). L'interprétation des variations de T/S est délicate par suite de l'élimination des iodures dans le milieu extérieur. Le jeûne peut également interférer avec cette élimination par modification du flux entrant d'iodures. Les variations précoces de T/S ne semblent pas être en rapport avec les événements constatés au niveau de la synthèse ou de la sécrétion des composés iodés. Malgré le faible taux d'hormones synthétisées dans la thyroïde, même après plusieurs jours, il faut souligner les phénomènes rapides mis en évidence au niveau de l'apparition des précurseurs marqués, des hormones et de la sécrétion de ces dernières dans le sang. Leur dégradation apparemment rapide au niveau périphérique tend à confirmer l'hypothèse d'une intense activité biosynthétique glandulaire, tout en expliquant les taux faibles de captation d'iode et de conversion hormonale. L'hétérogénéité fonctionnelle, ainsi mise en évidence, peut être la conséquence d'un métabolisme complexe au niveau folliculaire ou de l'existence de plusieurs populations folliculaires d'activités différentes.

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Trout Production and Eels in Bill Lake, Saguenay County, Quebec[1]

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O'CONNOR, J. F., AND G. POWER. 1973. Trout production and eels in Bill Lake, Saguenay County, Quebec. J. Fish. Res. Board Can. 30: 1398–1401.

Competition and predation by American eels (*Anguilla rostrata*) is believed to have substantially reduced trout population and production in Bill Lake. Brook trout (*Salvelinus fontinalis*) occurred at densities of 7/ha; biomass of 0.34 kg/ha and annual production was estimated at 0.21 kg/ha. This is considerably less than values for trout density, biomass, and production in other lakes in the Matamek watershed from which eels appear to be absent. Eels in Bill Lake are old and large but not numerous, in keeping with their apparent position as top carnivores.

O'CONNOR, J. F., AND G. POWER. 1973. Trout production and eels in Bill Lake, Saguenay County, Quebec. J. Fish. Res. Board Can. 30: 1398–1401.

Les auteurs sont d'avis que la compétition et la prédation par l'anguille d'Amérique (*Anguilla rostrata*) ont réduit de façon significative la population et la production d'ombles de fontaine (*Salvelinus fontinalis*) dans le lac Bill. L'omble de fontaine a une densité de population de sept individus par hectare, la biomasse est de 0.34 kg par hectare, et la production annuelle est estimée à 0.21 kg par hectare. Ces valeurs (densité, biomasse et production) sont beaucoup plus faibles que celles trouvées dans les autres lacs de la région de Matamek, où les anguilles semblent absentes. Les anguilles du lac Bill sont âgées et ont une grande taille, mais sont peu nombreuses, ce qui est en accord avec leur position apparente comme principaux carnivores.

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THIS note describes work done as part of a study of fish populations in the Matamek watershed. Bill Lake is located approximately 13 km NW of the mouth of the river (50°19′ N, 65°57′ W) and drains into the Matamek via the Muskrat River (Fig. 1). It has an area of 154 ha, a maximum depth of 34.5 m, and a shoreline of 7.9 km including islands. The lake is comparable to other lakes in the system, being oligotrophic and having a narrow littoral zone. Waterfalls prevent anadromous species from reaching the lake from the Gulf of St. Lawrence. It contains five species of fish: brook trout, *Salvelinus fontinalis*; rainbow smelt, *Osmerus mordax*; American eel, *Anguilla rostrata*; threespine stickleback, *Gasterosteus aculeatus*; ninespine stickleback, *Pungitius pungitius*. Compared to other lakes in the system, trout population and production appears to be limited by eel predation and competition.

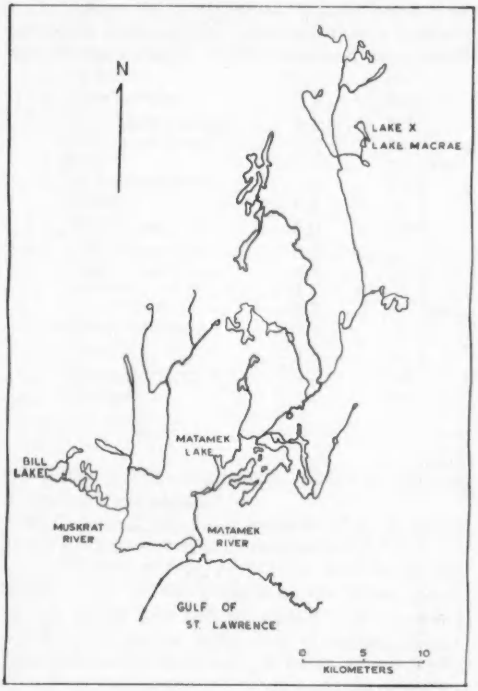

FIG. 1. The Matamek watershed, Saguenay County, Que.

Materials and methods — Three trapnets with 100-ft leaders, 1-inch stretched mesh wings and trap, were fished in Bill Lake for 66 days (June, July, and August) in 33 different locations. All suitable fish were anesthetized with M.S. 222 for marking and allowed to recover before release. Marking was done by injecting acrylic pigment subcutaneously in the lower jaw of trout or ventral side of eels. In August the lake was fished for 14 days using 11 gillnets ranging from 0.75- to 2.0-inch stretched mesh. Attempts to recapture marked eels by baited long line and eel traps were unsuccessful. Routine examination of all fish killed included analysis of stomach contents and collection of scales from trout and otoliths from eels for age determination. Brook trout were aged from scales (Cooper 1951). Growth rings on otoliths from eels were interpreted as described by Gray and Andrews (1971). The trout population was estimated using a modified Peterson estimate (Bailey 1951). Estimates were made for each age-class from 2+ to 5+. Confidence limits (95%) were calculated by treating R as a binomial, obtaining limits for R from the chart developed by Clopper and Pearson (1934) and substituting these in Bailey's (1951) formula. Ricker (1958) outlines the method. Allen's (1951) graphical method was used to estimate trout production.

Results — Age-frequency data for marked, recaptured, and total captured trout, together with the population estimates derived from these values are given in Table 1. No population estimate was possible for 1+ fish, but few are expected to be in the lake, since most trout under 2+ are resident in the surrounding streams. The final estimate has

TABLE 1. Population estimates of numbers of trout in various age-groups, Bill Lake, 1970. Final estimate includes trapnet mortalities.

Age	Marked	Marked recaptured	Total captured	Peterson estimate	95% Confidence interval	Final estimate
2+	93	3	32	710	330–2217	758
3+	72	29	117	272	204–407	277
4+	29	13	37	73	52–138	75
5+	18	3	13	60	26–595	62
6+	3	1	3	6		6

trapnet mortalities added. Bill Lake contained 7 trout/ha (3/acre). The standing crop was 0.34 kg/ha (0.30 lb/acre). Trout production is given in Table 2. Total annual production, 34.69 kg, is the sum of the estimates for each age-class. It is slightly low as the contribution of 1+ aged fish in the lake could not be estimated. Total production was 0.21 kg/ha (0.19 lb/acre).

Eels were captured only in trapnets. Although 2 out of 11 marked eels were recaptured during the marking period, no population estimate was possible. The eels were large compared to the trout and 23.1 kg of them were caught compared to an estimated total biomass of 55.3 kg for trout. Only 19 eels could be aged (Table 3). They ranged from 8 to 16 years and grew faster than the eel in Newfoundland studied by Gray and Andrews (1971). The length–weight relation for 33 eels, from 464 to 983 mm long, was $W = 0.00004\ L^{2.96}$ (W = weight g, L-length mm) (Fig. 2).

Discussion — Interspecific relations of trout and eels in Bill Lake during the summer season can be discussed in terms of diet, spatial distribution, and the impact of predation.

Table 4 provides a summary of the diet. The principal overlap was that each species ate sticklebacks. Resource sharing in the other categories was not great as different species were generally involved.

Analysis of stomach contents in the present study showed that trout occurred in 7 of 22 eel stomachs examined, and that, volumetrically, they were the major item in the diet of the eel. No evidence of other species preying on trout was found. In Bill Lake the eel has assumed the position of top carnivore and as such attains a large size but is relatively few in number.

Eels and trout were caught in trapnets at night when they appeared to move into the littoral area to feed. Such movements may contribute to competition and facilitate predation by the eels. The eel is a warmwater species active at summer temperatures and hibernating with the onset of winter (Smith and Saunders 1955). Hibernation of the

TABLE 2. Production in the trout population, Bill Lake, 1970.

Age	No. of fish	Growth (*g*)	Production (*kg/year*)	Production (*kg/ha/year*)
2+	758			
3+	277	41.6	21.05	0.13
4+	75	44.6	7.72	0.05
5+	62	55.1	3.53	0.02
6+	6	137.2	2.39	0.01
Total	1178		34.69	0.21

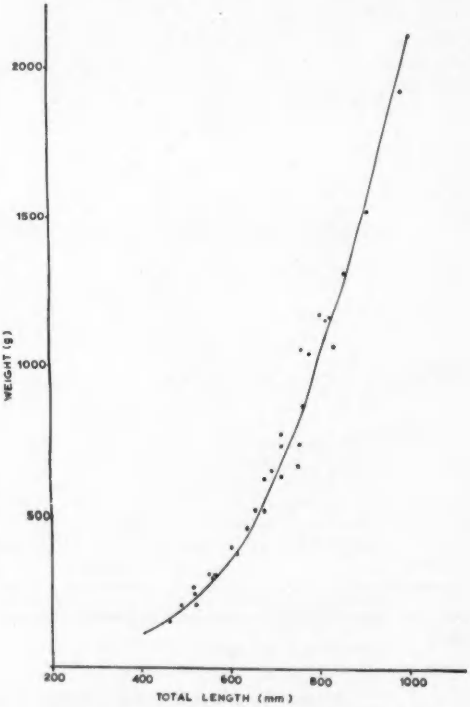

FIG. 2. Regression of weight on total length for eels from Bill Lake, 1970.

TABLE 3. Age and growth of American eel in Bill Lake, 1970.

Age (years)	8	9	10	11	12	13	14	15	16
No. of fish	2	7	3	1	2	2		1	1
Mean length (*mm*)	545	552	686	690	718	785		955	848
Mean weight (*g*)	289	300	700	660	690	1113		2115	1325

TABLE 4. Percent composition by bulk of food items in fish stomachs at Bill Lake, 1970.

Food items	Trout	Eels
Stickleback	31.1	20.9
Trichoptera larva	26.9	1.0
Lepidoptera larva	9.3	–
Digested invertebrates	6.6	0.5
Ephemeroptera nymph	3.8	–
Coleoptera imago	3.7	–
Odonata imago	2.8	–
Iris seeds	2.7	–
Diptera imago	2.0	0.5
Hymenoptera imago	1.8	2.1
Trichoptera imago	1.4	3.1
Smelt	1.2	2.1
Trichoptera pupa	1.2	3.1
Detritus	1.1	–
Brook trout	1.0	56.0
Other diptera larva	0.7	–
Chironomidae larva	0.5	–
Orthoptera imago	0.5	–
Coleoptera larva	0.3	–
Hemiptera imago	0.3	–
Arachnida	0.3	–
Odonata nymph	0.2	9.4
Gordioidea	–	1.0

eel during winter may prevent excessive reduction of the trout population.

The best indication of the effects of eel predation in Bill Lake comes from comparison with Matamek Lake, located a few kilometers east in similar terrain (Fig. 1) and containing the same species of fish except that eels are absent and there is a small population of Arctic char, *Salvelinus alpinus*. Matamek Lake contained 48 trout or 3.1 kg/ha (Saunders and Power 1970). At a higher elevation, Lake X, which contains only trout with severely restricted spawning areas, contained five trout or 1.6 kg/ha and Lake MacRae immediately adjacent with better spawning areas, contained 48 trout or 4.3 kg/ha (Carscadden 1970). These values are considerably higher than those for Bill Lake (seven trout, 0.34 kg/ha). In addition the mortality rate for Bill Lake trout between the 2+ and 3+ year-classes was twice the mortality rate at this stage reported for Matamek Lake by Saunders and Power (1970). The size of the trout in the eel stomachs indicates they belong to the 2+ age-class. Although the degree of predation by eels was not known, in the absence of other compensatory mechanisms, it must increase the mortality rate of the trout.

The weakness in these data was that direct predation could not be observed. Therefore, the extent of losses to the trout population in Bill Lake as a result of eel predation can only be estimated. The comparative data from other lakes and the high total biomass of eels caught in the trapnets compared to the estimated total biomass of trout in the lake indicate a potential for predation which could result in substantial reduction of the trout population.

Acknowledgments — This research was financed by the National Research Council of Canada and by Woods Hole Oceanographic Institution with funds provided in part by The Atlantic Foundation. We thank Mr D. Anions for his assistance in the field.

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Pressure-Sensing Ultrasonic Transmitter for Tracking Aquatic Animals

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Luke, D. McG., D. G. Pincock, and A. B. Stasko. 1973. Pressure-sensing ultrasonic transmitter for tracking aquatic animals. J. Fish. Res. Board Can. 30: 1402–1404.

A small transmitter (7 × 1.6 cm) for telemetering swimming depth of aquatic animals was developed. The transmitter operates for 3 days with a signal range of about 1 km in sea water. It codes depth to 40 m or more as changes in pulse repetition rates, detectable by standard ultrasonic receivers.

Luke, D. McG., D. G. Pincock, and A. B. Stasko. 1973. Pressure-sensing ultrasonic transmitter for tracking aquatic animals. J. Fish. Res. Board Can. 30: 1402–1404.

Nous avons mis au point un petit transmetteur (7 × 1.6 cm) permettant de télémesurer la profondeur de nage des animaux aquatiques. Le transmetteur peut opérer durant 3 jours avec une portée de 1 km dans l'eau de mer. Il codifie la profondeur jusqu'à 40 m sous forme de changements du taux de répétition des pulsations, décelables par des récepteurs ultrasoniques ordinaires.

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By methods previously reported for tracking aquatic animals by ultrasonic telemetry, only the horizontal components of movement could be studied (Stasko 1971) because swimming depth could not be measured directly except on very large animals. This shortcoming has limited the value of tracking studies in waters where temperature, salinity, oxygen concentration, chemical composition, illumination, and currents vary with depth.

The pressure-sensing transmitter described herein is the first unit small enough to be used in the gut of adult salmon and eels. It has performance characteristics similar to currently available location-only transmitters. The transmitter is a cylindrical capsule 7 × 1.6 cm (15 cc), weighing 17 g in water; it operates at 75 kHz with a battery life of about 3 days and signal range of about 1 km in sea water. Depth to 40 m is coded by pulse repetition rate of the signal (40–400 pulses/min); greater depths are possible with a different transducer. Pulse repetition rates vary linearly with depth. The range of pulse repetition rates can be compressed (e.g. 40–200 pulses/min) if counting up to 400 pulses/min proves too difficult.

Accuracy of the most recent prototype is ± 0.35 m over a range of depths from 0 to 40 m, maintained over temperatures 5–20 C. Cost of discrete components is approximately $80 for small quantities. A commercially manufactured version of the transmitter using thick film techniques will soon be available (Epitek Electronics, Ottawa). The acoustic signal radiation pattern in two planes is shown in Fig. 1; the units are db re 1 microbar at 1 m.

The pressure sensor (Kulite model TQL-360-50S; or model TQL-360-100S for depths to at least 70 m) uses a silicon diaphragm with diffused strain-gauge bridge mounted over a sealed reference air space. The transducer, as sold, is not compatible with salt water, but works well when protected by a 5-mm layer of silicone grease.

The tone-burst circuit in the transmitter (Fig. 2) is a squegging oscillator similar to that used by Thorson et al. (1969) with an output amplifier stage driving the piezoelectric transducer. Pulse repetition rate is varied by controlling the bias current to the oscillator transistor. The bridge output is interfaced to this control circuit by a difference amplifier with level shift. We use a Westinghouse WC788 micropower triple op-amp. The first two op-amps are connected as a high-gain difference amplifier with a gain of 101. As these amplifiers are a single integrated circuit their thermal drifts are closely matched and it can be shown that in this case the drifts of A1 and A2 cancel. The third op-amp has a gain of

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approximately 1.2 and gives a level shift of about −2 v with negligible thermal drift. The resistor controlling this level shift is the only component that has to be individually selected for each transmitter.

The pulse repetition rate is not very sensitive to battery voltage. Tests showed a shift corresponding to about 2 m depth for a one volt change, but the manufacturer's specifications for the 6.2-v silver-oxide battery show only a 0.2 v drop in the first 10% of rated life, a 0.1 v drop in the next 80% of life, and then a very rapid fall at the end.

Nine of these transmitters have been used to track 4-kg adult Atlantic salmon ascending an estuary (four fish for a total of 53 hr) and 2-kg adult American eels descending an estuary (five fish for a total of 64 hr); the longest single tracking lasted 34 hr. Field and laboratory tests showed that the transmitters register depth equally well from inside the fish's stomach and from outside the fish.

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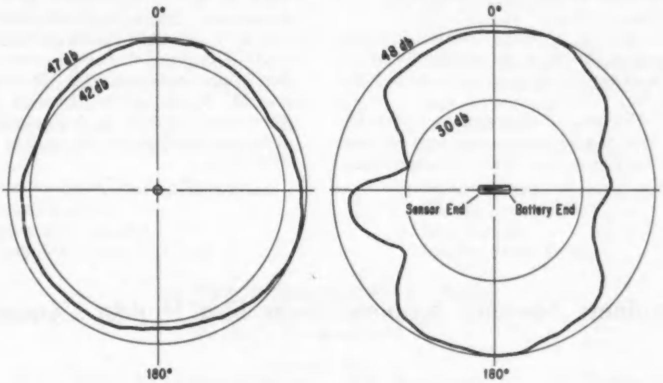

FIG. 1. End and side views of acoustic signal radiation pattern of transmitter (at center of each pattern).

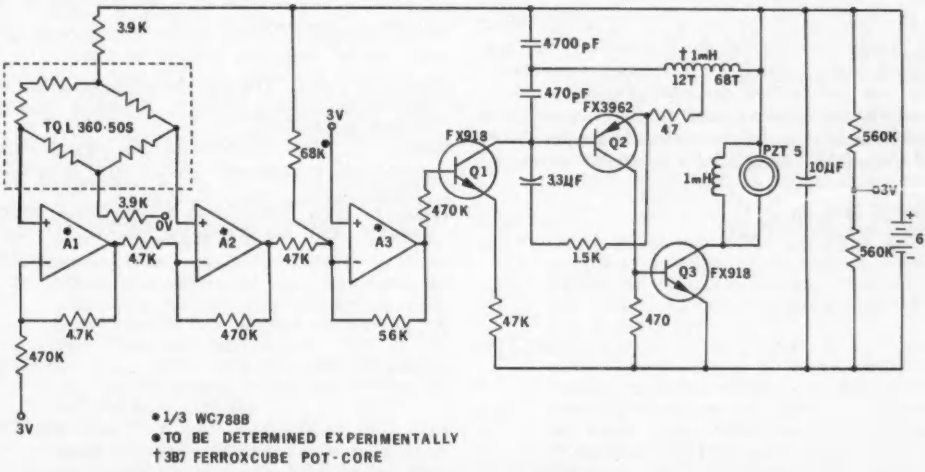
3.9K
TQ L 360·50S
3.9K
0V
A1
A2
A3
4.7K
47K
4.7K
470K
56K
470K
3V
3V
68K
FX918
Q1
470K
47K
4700 pF
470pF
† 1mH
12T
68T
FX3962
Q2
47
3.3µF
1.5K
470
PZT 5
1mH
10µF
Q3
FX918
560K
3V
560K
6V
• 1/3 WC788B
• TO BE DETERMINED EXPERIMENTALLY
† 3B7 FERROXCUBE POT-CORE

FIG. 2. Schematic of the transmitter.

Institute of the University of New Brunswick for their encouragement and assistance. Acoustic tank tests of radiation patterns were done by Defence Research Establishment Atlantic, Dartmouth, N.S.

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Addendum: Mercury Removal from Fish Protein Concentrate

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(*Ref. J. Fish. Res. Board Can. 29: 1777–1779, 1972*)

THE following statement was inadvertently omitted in the last paragraph on p. 1778, after "Since the normal process did not remove the mercury, a more severe system for extraction was tried": This was the method described by Zitko (1971), in which the benzene used in the extraction of methylmercury in the methods of Westöö (1966) and Gage (1961) is replaced with alcohol to remove the mercury compounds from the proteins in the presence of hydrochloric acid.

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Recent Articles on FRB Investigations Published in Other Periodicals

Until 1970, reprints of these articles had been included in an annual volume of "Studies," composed of two parts. The final binding was the 1969 Studies, Part 2, which included No. 1355. These are no longer bound and distributed. We continue, however, to number and list all articles, which henceforth may be obtained in reprint form only from the author or originating FRB establishment. The number following each title refers to the FRB establishment listed below.

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(8) Fisheries Research Board of Canada
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Halifax, Nova Scotia

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St. John's, Newfoundland

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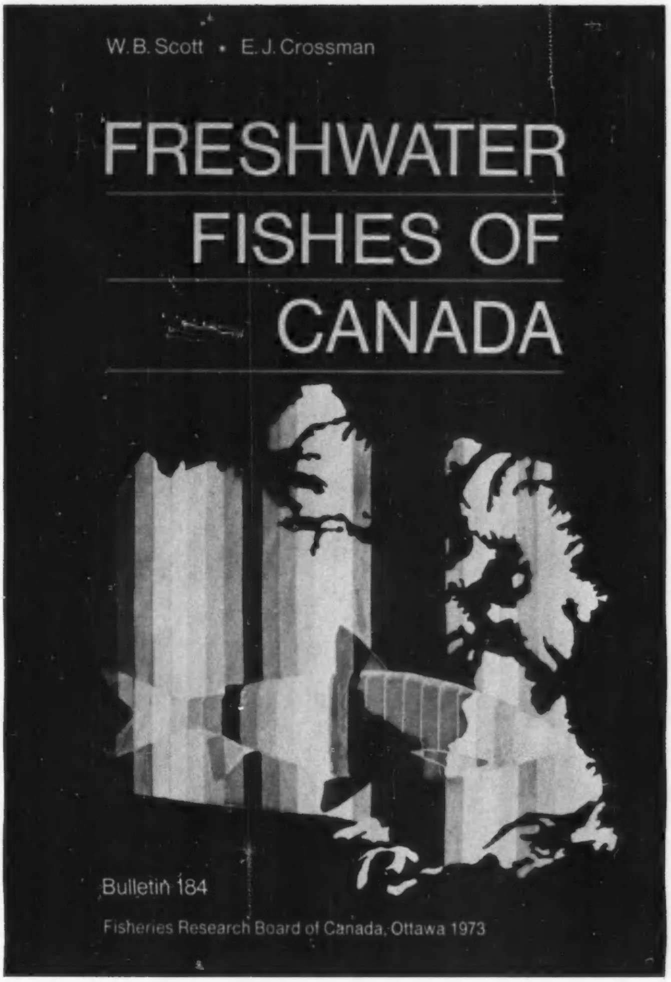
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